TESIS DOCTORAL

# Dynamics of the species ranges in a changing climate

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# PREFACE

This thesis is the result of a four-year PhD project based at the National Museum of Natural Sciences (MNCN-CSIC) and University Rey Juan Carlos (URJC) in Madrid, Spain. The project was supervised by Prof Dr Miguel B. Araújo. The work was funded by the Ministry of Economy and Competitiveness through research projects CGL2015-68438-P and PGC2018–099363-B-I00.

The thesis consists of four chapters, a General Introduction and a Synthesis. The general introduction describes the background and aims of the thesis, and the Synthesis summarises the main findings and discusses the work presented from a broader perspective.

Four other chapters are the core of the thesis. The first one is a synthesis paper (Chapter I), two analytical papers (Chapter II & Chapter IV) and one software note (*climetrics* R package – Chapter III) to measure multiple dimensions of climate change. At the time of submission, two papers were published as scientific articles, one is near submission and the fourth is in preparation.

Shirin Taheri

Madrid, June 2022

*To all the brave women and men who fight for freedom*

*equality and human right*

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# ARTICLE REFERENCES

## CHAPTER (I)

**Taheri, S.,** Naimi, B., Rahbek, C., Araújo, M. B. (2021). Improvements in reports of species redistribution under climate change are required. Science Advances, 7(15).  DOI: 10.1126/sciadv.abe1110

## CHAPTER (II)

**Taheri, S**., García-Callejas, D., Araújo, M. B. (2021). Discriminating climate, land-cover and random effects on species range dynamics. Global Change Biology, 6(27). https://doi.org/10.1111/gcb.15483

## CHAPTER (III)

**Taheri, S**., Naimi, B., Araujo, M.B. Climetrics: R package to quantify multiple dimensions of climate change. (*Near submission*).

## CHAPTER (IV)

**Taheri, S**., Araújo, B. M. Exposure of global threatened species distributions to climate and land-use changes over the past century. (*In preparation)o*

# SUMMARY

## Background

Evidence is mounting that ongoing climate change is leading to a globally consistent fingerprint of systematic shifts in species distributions, and they are estimated to be 2.5 times greater than previously anticipated. In particular, a series of commonly articulated hypotheses have emerged that species are expected to shift their distributions to higher latitudes or elevations, and deeper depths in response to climate change, reflecting an underlying assumption that species will move to cooler locations to track spatial changes in the temperature. However, many species are not demonstrating range shifts consistent with these hypotheses, because species do not necessarily move along the linear temperature gradients. Their distributions are influenced by many interconnected factors, such as precipitation, land-use change, physical barriers, species trait, population dynamics, invasive species, interspecific species interactions and microclimate conditions.

Understanding how species distribution changes in response to climate change is enormously complex. Providing effective explanations for the observed variability in species’ range shifts requires, firstly, that method used for detection of distributional changes are able to distinguish between directional and non-directional changes and secondly, that they are able to distinguish distributional changes driven by natural population dynamics from changes driven by external forcing (climatic or non-climatic).

## Objectives

Considering carefully all the known challenges, this thesis asks how appropriate are methods commonly used to detect shifts in species distribution and provides an updated synthesis of climate-related range shift studies. The main objective of this thesis is to explore uncertainties associated with data and methods used to measure species range dynamics. The specific objectives are as follows: first, to evaluate the climate-related range shifts studies to identify the robustness of the inferences linking distributional changes tightly with climate changes (Chapter I). Second, to explore the role of climate, land cover and random effect in the different sections of the species distribution (Chapter II). Third, to develop a platform to quantify multiple dimensions of climate change (Chapter III). Forth, to quantify the exposure of global threatened species distribution to multiple dimensions of climate and land-use change (Chapter IV).

## Methodology

To evaluate the robustness of the methods linking distributional shifts with climate, 240 scientific reports were reviewed and classified based on simple criteria related to the minimum standards that should be required to attribute range shifts to climate change. The criteria asked whether observed distributional shifts are compared against random expectations, whether multicausal factors are examined on equal footing, and whether studies provide sufficient documentation to enable replication.

For the second objective and to explore the mechanisms behind species range shift, I used historical range dynamics among data from the observed distribution of 82 breeding birds in Great Britain against three alternative models; climate change models, assuming that distributions changed following climate changes; land-cover change model, assuming that species distributions changed following land-cover changes; and a null model that, while keeping the same quantities of observed distributional changes (expansions and contractions), randomized the direction of the changes.

To facilitate modelling the complexity of climate changes, this thesis developed the "Climetrics" R package to uncover multiple dimensions of climate change. Six widely used metrics of climate change were implemented in this R package using the methods in published articles. The six climate change metrics were developed in this thesis are 1) Standardized local anomalies; 2) Changes in probability of local climate extremes; 3) Change in area of analogous climates; 4) Novel climates; 5) Change in the distance to analogous climates, and 6) Climate change velocity.

To quantify the exposure of threatened species distribution to climate and land-use change, this thesis mapped ten risks from five climate change dimensions and five land-use transitions and compared the ensuing patterns with diversity patterns among threatened amphibians, birds, mammals, reptiles, and plants species. Then the proportion of threatened species that were impacted by multiple dimensions of climate and land-use change were calculated.

## Results

The results of Chapter (I) found that only ~12.1% of studies compare distributional shifts across multiple directions, ~1.6% distinguish observed patterns from random expectations, ~19.66% examine multi-causal factors and 25% not provided sufficient data and results to allow replication. The comparison of observed range shifts with projections arising from the three alternative models in Chapter (2) revealed that determinants of species range shifts were seemingly variable across each one of the four predefined sections of the range. While rear edges of northerly distributed species have shifted consistently with projections from a climate-driven model, shifts at the leading edge of southerly distributed species carry a stronger imprint of land-cover change. In contrast, shifts at the leading edges of northerly distributed species and the rear edges of southerly distributed species that is, distributions at both the northern and southern tips of Great Britain were no different from that expected by chance. Mapping risks from multiple dimensions of climate and land-use shows (Chapter 4) shows that 10% of globally threatened species face an extremely high risk for both climate and land-use change over the last century. In general, the threatened species in the Caribbean and Latin America, as well as Southeast and South Asia, were exposed to the greatest amount of co-occurring threats.

## Conclusion

Despite repeated calls for better integrations of multiple drivers, studies on climate-related range shifts are mostly univariate and unidirectional. In general, the findings demonstrate substantial improvements should be considered in biodiversity assessments under climate change. The chapters of

this thesis encourage study designs that account for multiple drivers on equal footing and appropriate pattern detection methods in range shift studies. The thesis also discusses the exposure of global threatened species distribution to multiple risks associated with climate change complexity and historical land-use change over the past century, with unequal spatial pattern around the world.

This thesis provides a hint of the best-practice standard needed for assessments of climate-related range shifts. Future investigations should seek to expand the facets of biodiversity change considered in quality assessments and strive to build consensus on the standards required to increase the strength of evidence of climate change impacts on biodiversity while developing detailed guidelines to help increase the robustness, transparency, and reproducibility of the climate -related range shifts assessments.

# RESUMEN

## Antecedentes

Cada vez hay más pruebas de que el cambio climático en curso está dando lugar a una huella global de cambios sistemáticos en la distribución de las especies, y se estima que son 2,5 veces mayores de lo previsto anteriormente. En particular, han surgido una serie de hipótesis comúnmente articuladas según las cuales se espera que las especies desplacen sus distribuciones a latitudes o elevaciones más altas y a profundidades mayores en respuesta al cambio climático, lo que refleja una suposición subyacente de que las especies se desplazarán a lugares más fríos para seguir los cambios espaciales de la temperatura. Sin embargo, muchas especies no están demostrando desplazamientos del área de distribución coherentes con estas hipótesis, porque las especies no se mueven necesariamente a lo largo de los gradientes lineales de temperatura. Sus distribuciones están influidas por muchos factores interconectados, como las precipitaciones, los cambios en el uso del suelo, las barreras físicas, los rasgos de las especies, la dinámica de las poblaciones, las especies invasoras, las interacciones entre especies y las condiciones microclimáticas.

Entender cómo cambia la distribución de las especies en respuesta al cambio climático es enormemente complejo. Para explicar eficazmente la variabilidad observada en los cambios del área de distribución de las especies es necesario, en primer lugar, que el método utilizado para detectar los cambios de distribución impulsados por la dinámica natural de la población de los cambios impulsados por fuerzas externas (climáticas o no climáticas).

# Objetivos

Considerando detenidamente todos los retos conocidos, esta tesis se pregunta hasta qué punto son apropiados los métodos que se utilizan habitualmente para detectar los cambios en la distribución de las especies y ofrece una síntesis actualizada de los estudios sobre cambios en el área de distribución relacionados con el clima. El objetivo principal de esta tesis es explorar las incertidumbres asociadas a los datos y métodos utilizados para medir la dinámica del área de distribución de las especies.

Los objetivos específicos son los siguientes: en primer lugar, evaluar los estudios sobre cambios de distribución relacionados con el clima para identificar la solidez de las inferencias que vinculan estrechamente los cambios de distribución con los cambios climáticos (capítulo I). En segundo lugar, explorar el papel del clima, la cobertura del suelo y el efecto aleatorio en los distintos tramos de la distribución de las especies (capítulo II). En tercer lugar, desarrollar una plataforma para cuantificar las múltiples dimensiones del cambio climático (capítulo II). En cuarto lugar, cuantificar la exposición de la distribución global de las especies amenazadas a las múltiples dimensiones del cambio climático y del uso del suelo (Capítulo IV).

## Metodología

Para evaluar la solidez de los métodos que relacionan los cambios de distribución con el clima, se revisaron 240 informes científicos y se clasificaron en función de criterios sencillos relacionados con las normas mínimas que deberían exigirse para atribuir los cambios de distribución al cambio climático. Los criterios se referían a si los cambios de distribución observados se comparaban con expectativas aleatorias, si los factores multicausales se examinaban en igualdad de condiciones y si los estudios proporcionaban suficiente documentación para permitir su repetición.

Para el segundo objetivo, y con el fin de explorar los mecanismos que subyacen a los cambios de distribución de las especies, utilicé la dinámica histórica del área de distribución entre los datos de la distribución observada de 82 aves reproductoras en Gran Bretaña frente a tres modelos alternativos: modelos de cambio climático, en los que se asumía que las distribuciones cambiaban tras los cambios climáticos; modelo de cambio de la cobertura del suelo, en el que se asumía que las distribuciones de las especies cambiaban tras los cambios de la cobertura del suelo; y un modelo nulo que, manteniendo las mismas cantidades de cambios de distribución observados (expansiones y contracciones), aleatorizaba la dirección de los cambios.

Para facilitar la modelización de la complejidad de los cambios climáticos, esta tesis desarrolló el paquete R "*Climetrics*" para descubrir múltiples dimensiones del cambio climático. En este paquete R se implementaron seis métricas de cambio climático ampliamente utilizadas utilizando los métodos de los artículos publicados. Las seis métricas del cambio climático desarrolladas en esta tesis son: 1) Anomalías locales estandarizadas; 2) Cambios en la probabilidad de extremos climáticos locales; 3) Cambio en el área de climas análogos; 4) Climas nuevos; 5) Cambio en la distancia a climas análogos, y 6) Velocidad del cambio climático.

Para cuantificar la exposición de la distribución de las especies amenazadas al cambio climático y de uso del suelo Para cuantificar la exposición de la distribución de las especies amenazadas al cambio climático y de uso del suelo, en esta tesis se trazaron diez riesgos a partir de cinco dimensiones del cambio climático y cinco transiciones de uso del suelo y se compararon los patrones resultantes con los patrones de diversidad entre las especies amenazadas de anfibios, aves, mamíferos, reptiles y plantas. A continuación, se calculó la proporción de especies amenazadas que se vieron afectadas por las múltiples dimensiones del cambio climático y de uso del suelo.

## Resultados

Los resultados del capítulo (I) revelaron que sólo el ~12,1% de los estudios comparan los cambios de distribución en múltiples direcciones, el ~1,6% distinguen los patrones observados de las expectativas aleatorias, el ~19,66% examinan los factores multicausales y el 25% no proporcionaron suficientes datos y resultados para permitir su replicación. La comparación de los desplazamientos del área de distribución observados con las proyecciones derivadas de los tres modelos alternativos del capítulo (II) reveló que los determinantes de los desplazamientos del área de distribución de las especies eran aparentemente variables en cada una de las cuatro secciones predefinidas del área de distribución. Mientras que los bordes posteriores de las especies de distribución septentrional se han desplazado de forma coherente con las proyecciones de un modelo basado en el clima, los desplazamientos en el borde anterior de las especies de distribución meridional llevan una huella más fuerte del cambio de la cubierta vegetal. Por el contrario, los cambios en los bordes de ataque de las especies de distribución septentrional y en los bordes posteriores de las especies de distribución meridional, es decir, las distribuciones en los extremos norte y sur de Gran Bretaña, no difieren de lo esperado por el azar. La cartografía de los riesgos derivados de las múltiples dimensiones del clima y del uso del suelo (capítulo IV) muestra que el 10% de las especies amenazadas a nivel mundial se enfrentan a un riesgo extremadamente alto tanto por el cambio climático como por el de uso del suelo durante el último siglo. En general, las especies amenazadas en el Caribe y América Latina, así como en el sudeste y el sur de Asia, fueron las más expuestas a las amenazas concurrentes.

## Conclusión

A pesar de los reiterados llamamientos a una mejor integración de los múltiples impulsores, los estudios sobre los cambios de área de distribución relacionados con el clima son en su mayoría univariantes y unidireccionales. En general, los resultados demuestran que deberían considerarse mejoras sustanciales en las evaluaciones de la biodiversidad bajo el cambio climático. En los capítulos de esta tesis se fomenta el diseño de estudios que tengan en cuenta los múltiples impulsores en igualdad de condiciones y los métodos adecuados de detección de patrones en los estudios sobre los cambios del área de distribución. La tesis también analiza la exposición de la distribución global de las especies amenazadas a múltiples riesgos asociados a la complejidad del cambio climático y al cambio histórico del uso del suelo en el último siglo, con un patrón espacial desigual en todo el mundo.

Esta tesis ofrece un indicio del estándar de buenas prácticas necesario para evaluar los cambios de distribución relacionados con el clima. Las investigaciones futuras deberían tratar de ampliar las facetas del cambio de la biodiversidad que se tienen en cuenta en las evaluaciones de calidad y esforzarse por llegar a un consenso sobre las normas necesarias para aumentar la solidez de las pruebas de los impactos del cambio climático en la biodiversidad, al tiempo que se desarrollan directrices detalladas que ayuden a aumentar la solidez, la transparencia y la reproducibilidad de las evaluaciones.

# GENERAL INTRODUCTION

Species are highly mobile in their distributional range, often shifting, expanding and contracting over time and space (MacArthur, 1972). Understanding the factors determining the distributional shifts has been a major focus throughout the history of ecology (Grinnell, 1917; MacArthur, 1972; Gaston, 2003; Sexton et al., 2009; McCaslin & Heath, 2020).

In recent years, there has been an upsurge of interest in analysing dynamics in species' ranges. Shifts in species distributions toward traditionally cooler climes are attributed to recent climate warming (e.g., Parmesan et al., 1999; Thomas & Lennon, 1999; Breed et al., 2013; Morueta-Holme et al., 2015).

A recent meta-analysis (I.-C. Chen et al., 2011) found that latitudinal and altitudinal shifts of species ranges have been 2.5 times greater than previously reported (Parmesan & Yohe, 2003), although to great levels of variation within and across taxonomic groups. While many studies have reportedly shown non-random shifts in latitude and altitudinal changes toward pole or higher elevation (Parmesan et al., 1999; Pounds et al., 1999; Thomas & Lennon, 1999; Delava et al., 2014), some provide evidence that species lag behind climate change (Devictor et al., 2008; Ash et al., 2016; Alexander et al., 2018), and that distributional shifts can be seemingly idiosyncratic (VanDerWal et al., 2013; Gillings et al., 2014; Taheri et al., 2016), or some species have not shifted their range at all (Zhu et al., 2012).

The complexities in species responses to climate change can obscure patterns, making it difficult to infer the effects of climate change on species distributions. We do not, for example, have a clear understanding of the inferred species responses to the stochastic changes in dynamics of populations or the responses to unaccounted factors.

The *a priori* expectation and commonly-held hypothesis is that species should shift poleward or upward in response to rising temperature or isotherm shifts (Tingley et al., 2009; Nicastro et al., 2013). However, an increase in temperature is likely to have a directional impact on species range shifts because temperature changes with latitude (cooler conditions in higher latitude/elevation and warmer conditions in lower latitude/elevation). Therefore, one expects isothermal and mostly unidirectional poleward or upward shifts as the climate warms. Indeed, the unidirectional (poleward/upward) and univariate (temperature only) perspectives on climate-driven range shifts ignore the fact that climate isotherm in some areas may be shifting in the opposite direction than expected (Pinsky et al., 2013; VanDerWal et al., 2013; Lenoir & Svenning, 2014; Taheri et al., 2021) or in longitudes instead of simple latitude. A consideration of the multidimensional nature of climate change is also recommended (Garcia et al., 2014) because different dimensions of climate change affect biodiversity in different ways; for example, not all species are at equal risk of climate change velocity (Davies et al., 2009). Strong disperses should be most able to maintain distributional equilibrium with climate conditions and are therefore likely to occupy more of their potential range and avoid extinction (Sandel et al., 2011). Local climate extremes such as extreme events or standardized local anomalies are expected to alter the distribution of the population of individual species or community responses such as changes to species richness, composition or dominance (Smale & Wernberg, 2013; I. Harris et al., 2020).

In addition, measuring climate-induced range shifts is sensitive to methods and data. For example, analysing the southernmost or northernmost marginal cells of breeding British birds suggested northward shifts by ~18 km during the 20th century (Thomas & Lennon, 1999). The analysis of CTI (Community Temperature Index) showed that birds lag 182±53 km behind changes in climate (Devictor et al., 2008), and the use of climate velocity (the temporal and spatial trend in temperature and precipitation) showed range shifts among Australian birds were idiosyncratic and followed climate velocity (VanDerWal et al., 2013).

An accurate diagnosis of the effects of climate change on the distributions of species requires, firstly, that methods used for detection of distributional changes can distinguish between directional and non-directional changes and, secondly, that they can tease apart distributional changes driven by natural population dynamics from changes driven by external forcing (climatic or non- climatic) (Taheri et al., 2016)

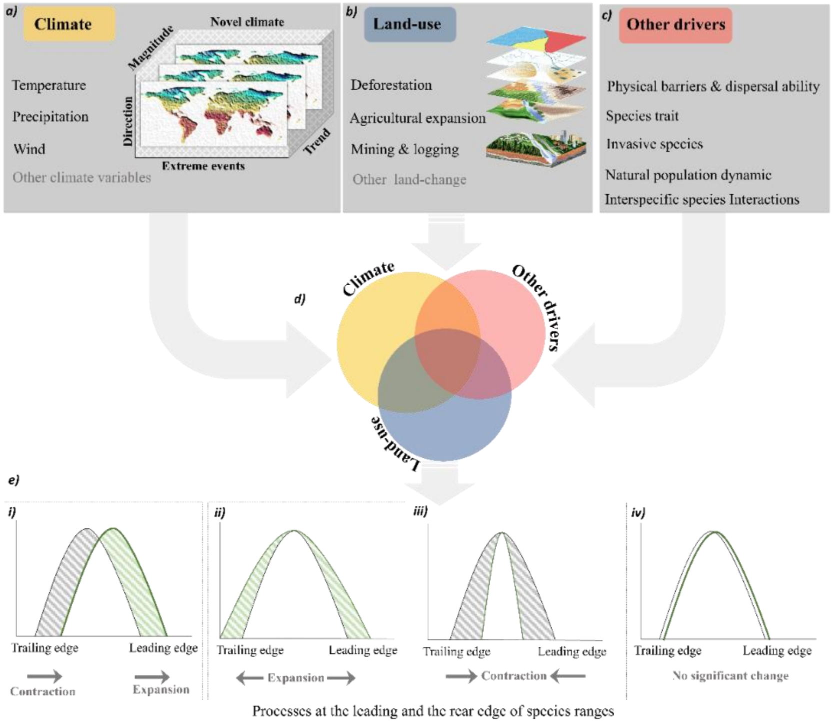

**Fig 1.**Schematic diagram of possible drivers of species ranges shifts on the location of range boundary. (a) Illustrates climate as a complex phenomenon; the climate cube shows multiple parameters across multiple geographic and temporal scales and different dimensions of climate change (e.g., magnitude of climate change, novel climates, velocity etc.). (b) Shows land degradation due to the human influence that also impacts species ranges. (c) Represent some other types of pressures that may cause range shifts, including: population dynamic, interspecific species interaction, physical barriers and species trait (e.g., dispersal ability, body size etc.). (d) the possible interaction of driving forces on species range shifts. (e) Examples of four possible changes in range margins of species, edge expansion and trailing edge contraction (i); expansion in both trailing and leading edge (ii); or contraction in both leading leading and trailing edge (iii); no significant change in range margins (iv).

The overall objective of this thesis is to investigate some of the above challenges and discusses uncertainties associated with data and methods in climate-induced range shifts. In addition, this thesis suggests a comprehensive assessment for the detection and attribution of observed biological changes caused by multifaceted drivers (Fig .1).

In particular, in this thesis the following objectives are addressed:

**I.** To evaluate the climate-related range shifts reports and identify the robustness of the inferences linking distributional changes tightly with climate changes.

**II.** Discriminating climate, land-cover and random effects on species range dynamics.

**III.** To develop a platform to quantify multiple dimensions of climate change.

**IV.** To quantify the exposure of global threatened species distribution to multiple dimensions of climate and land-use change.

Chapter (I) (Taheri et al., 2021) evaluates 240 climate-related range shift studies using simple criteria related to the minimum standards that should be required to attribute range shifts to contemporary climate change. The three main criteria revolve around the detection and attribution of climate-related range shifts and the reproducibility of studies.

For pattern detection and attribution, the focus is on the methodological aspects of the studies, and to explore how the species' distributional shifts are measured. In particular, the question for pattern detection is whether distribution shifts are analysed across all potential directions (e.g., latitude, longitude, and elevation), and whether the null expectation regarding distributional changes (likelihood of changes derived from patterns shifted by chance because of internal variability) is determined.

The question for attribution is whether studies examined potential causal links between observed distributional changes and environmental predictors (e.g., climate, precipitation, and land use). For this question, all studies are reviewed to assess how (if at all) they attributed observed shifts in species distributions to climate change and what approaches are used to perform the task. The papers that investigated multiple alternative causal factors on equal footing, rather than simply examining patterns against a single predictor (e.g., temperature), receive a maximum score for the attribution criteria.

For reproducibility, the focus is on results. A study receives the full score for this group if the results are available for each individual species analysed and if the divergence responses among species are fairly reported.

The updated synthesis provided in this chapter helped to understand the current state of the art on knowledge gap and methodological shortfalls in the fast-moving research on climate-related range shifts. The experiences from Chapter (I) aided in developing Chapter (II).

In Chapter (II) (Taheri et al., 2020) the focus turns to the range dynamics and their underlying causes. This chapter examines historical range dynamics among 82 bird's species in Great Britain against three alternative models: climate change model, assuming that distributions changed following climate changes; land-cover change model, assuming that species distributions changed following land-cover changes; and a null model that, while keeping the same quantities of observed distributional changes (expansions and contractions), randomized the direction of the changes.

In particular, the chapter examines whether observed range shifts in the distribution of birds are best explained by climate and historical land-cover change, or whether they are not distinguishable from what would be expected by chance (stochasticity in population dynamics). This chapter independently examines four sections of species distributions: leading and rear edges of the southern and northernmost edges of southerly and northerly-distributed species. The analysis is repeated across a twenty-year period (1968-72 vs. 1988-91) and a forty-year period (1968-72 vs. 2007-11).

Climate is a multivariate and multidimensional phenomenon. Adequately capturing the wealth of climate change manifestations and the different ways it interacts with the living systems requires that its multiple dimensions be appropriately characterised through alternative, metrics.

Chapter (III) Presents a platform to quantify different dimensions (metrics) of climate change. This chapter gathers six common climate change metrics as an extensible, reproducible and user-friendly R Package called "*Climetrics*". The package should provide a set of useful tools to map the complexity in climate change using multivariate climate parameters and more sophisticated methods.

Chapter (IV) quantifies the exposure of global threatened species distribution to multiple dimensions of climate change (using the "Climetrics" R package) and historical land-use change over the past century. This chapter illustrates the global distribution of risks, using multiple dimensions of climate change (temporal slope of temperature & precipitation; standardized local anomalies; velocity of climate change & extreme events) and historical land dynamics (forest loss, crop gain, land frequency change and pasture gain) as well as urbanization as threats to global's threatened reptiles, plants, mammals, birds and amphibians over the past century. Then provides a global estimation of high-risk areas for threatened species due to the concurrent impact of climate and land-use change over the 20th century and calculated the proportion of threatened species in areas with extremely high to low risk of climate and land-use change in isolation and combination in each Köppen-Geiger climate classification.

# I CHAPTER. IMPROVEMENTS IN REPORTS OF SPECIES REDISTRIBUTION UNDER CLIMATE CHANGE ARE REQUIRED

Shirin Taheri*; Babak Naimi; Carsten Rahbek; Miguel B. Araújo*

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# Improvements in reports of species distribution under climate change are required

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## Abstract

Studies have documented climate-change-induced shifts in species distributions but uncertainties associated with data and methods are typically unexplored. We reviewed 240 reports of climate-related multiple-species range shifts and classified them based on three criteria. We ask if observed distributional shifts are compared against random expectations; if multi-causal factors are examined on equal footing; and if studies provide sufficient documentation to enable replication. We found that only ~12.1% of studies compare distributional shifts across multiple directions, ~1.6% distinguish observed patterns from random expectations and ~19.66% examined multi-causal factors in equal footing. Finally, ~75.5% of studies report sufficient

data and results to allow replication. We show that despite gradual improvements over time, reports of climate-induced change in species distributions require substantial scope for raising standards in data and methods. Accurate reporting is important because policy responses depend on them. Flawed assessments can fuel criticism and divert scarce resources for biodiversity to competing uses and priorities.

## Introduction

As climate changes, so do species distributions. Evidence is mounting that ongoing climate changes are causing species to redistribute globally (Parmesan, 2006; I.-C. Chen et al., 2011). The magnitude of distributional shifts is now estimated to be 2.5 times greater than originally thought (Parmesan & Yohe, 2003). While many studies have uncovered the existence of non-random latitudinal or altitudinal shifts in species distributions (Parmesan et al., 1999; Thomas & Lennon, 1999; Parmesan & Yohe, 2003), consistent with the hypothesis that climate change is driving them, others found that shifts can lag behind climate change owing to physiological plasticity, microclimate buffering, and delayed responses (Pounds et al., 1999; Devictor et al., 2008; Forero-Medina et al., 2011). Such lags can lead to non-detection of ongoing distributional changes as well as failures to detect the mechanisms underpinning them. Observational studies have also detected species redistributions not following clear climatic gradients (Archaux, 2003; Bedford et al., 2012; VanDerWal et al., 2013). Such seemingly idiosyncratic responses to climate change could be related to complex interactions among temperature, precipitation (Tingley et al., 2012), land-use change (Crimmins et al., 2011), species climatic tolerances(Warren et al., 2001), and biotic interactions (M. B. Araújo et al., 2013). Complex non-linear species responses to climate change can also limit the ability to detect distributional changes.

This is particularly true with approaches assuming simple, often linear, relationships between temperature and species distributions (VanDerWal et al., 2013). Measuring range dynamics along spatial gradients, such as latitude or altitude, can also mask complex biological responses to climate change because such gradients are not precise surrogates for temperature gradients let alone for multiple climate dimensions (Hersteinsson & MacDonald, 1992; Hawkins & Felizola Diniz-Filho, 2004). Unlike the literature involving modelling of future climate change effects on species distributions, where several studies have examined uncertainties and addressed questions related to the minimum standards that should be required to make statements about modelled patterns (M. B. Araújo et al., 2019; Zurell et al., 2020), there is a surprising lack of analyses evaluating the quality of observational inferences regarding climate change effects on past species distributions. As a first step towards weighting the strength of the observational evidence provided by such studies, we review the literature involving the analysis of multiple species responses to climate change (see methods; Fig. A 1.1) in light of three important criteria: 1) pattern detection, or the ability to discern signal from noise in patterns of species distributional shifts; 2) causality, or the ability to attribute climate change as the most plausible driver of observed distributional shifts given alternative mechanisms; and 3) reproducibility, or the ability to replicate studies given the information provided.

Each one of these criteria is assessed by simple ‘yes’ or ‘no’ answer to six questions linked with the three criteria (Box 1). Stronger support to the conclusions in the reviewed studies is expected for those comparing distributional changes across multiple geographical directions, investigating multiple alternative causal mechanisms potentially driving distributional changes, and describing results with enough detail so as to enable replication and reanalysis.

**Box 1.** Checklist used to measure the strength of evidence about species distributional shifts and their link with climate.

**Evaluation Criteria**

**Question of interest**: Are distributional changes different from that expected in the absence of major external drivers, that is, by chance?

**I. Pattern detection**

*a.* Are range changes analyzed simultaneously across all possible directions of change?
Yes =1, No =0
*b.* If so, are the obtained results compared against a null model expectation enabling distinguishing the observed patterns from chance expectation? Yes =1, No =0

**Question of interest**: Are potential causal factors rather than temperature examined in equal footing?

**II. Attribution**

*a.* Are explanatory causes of range changes investigated? Yes =1, No =0
*b.* If so, are alternative causal explanations compared on equal footing?
Yes =1, No =0

**Question of interest:** Are distributional changes described with sufficient details to enable replication and reanalysis of the results?

**III. Reproducibility**

a. Are results presented for each individual species? Yes =1, No =0
*b.* If not, is variation among range dynamics of different sets of species described? Yes =1, No =0

# Results

Using extensive search of the literature (see methods), we identified 240 studies examining the effects of climate change on the distributions of multiple species. Existing research is strongly biased towards the northern hemisphere (78.9%) and terrestrial ecosystems (80.4%) (Fig.I.1a). Specifically, studies predominate in North America and Europe, mainly western Europe and within it the UK, with significant knowledge gaps emerging in South America, Africa, Asia and the Middle East (See also Lenoir & Svenning, 2014).

We also found that evidence of climate change effects on species distribution has been examined for ≤ 2 % of Reptiles, Insects, Plants, Algae, Crustacean and Mollusca, 2.9 % Mammals 2.3 % Fishes and 23.47 % of bird species (Fig.I.1b).

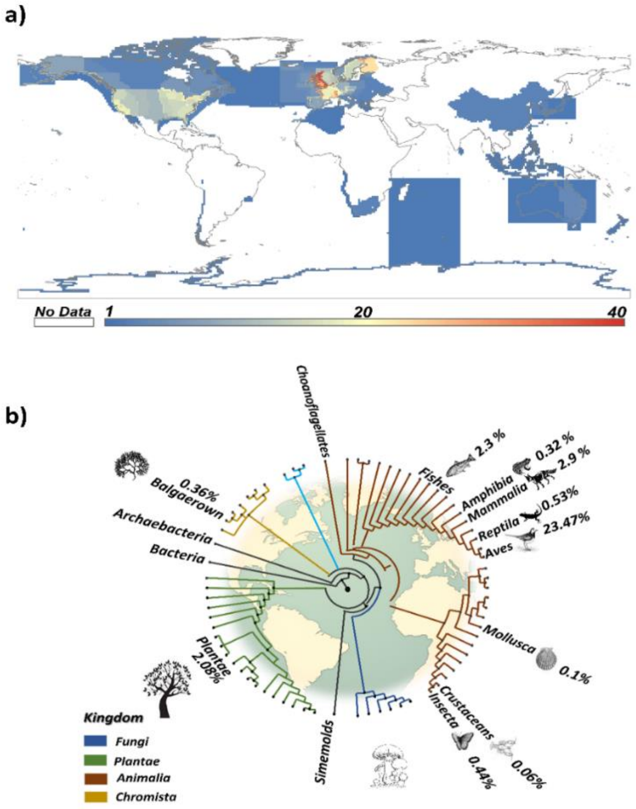

**Fig I.1**. Geographic and taxonomic coverage of climate related range shifts studies. a) geographical coverage across terrestrial and marine realms with 82% of the studies being in the northern hemisphere while 80.4% covering terrestrial ecosystems; b) taxonomic coverage with ≤ 2% including studies with amphibians, insects, reptiles, algae, crustaceans, and mollusca, 2.3% including fish, 2.9 % mammals, and 23.47% birds.

When examining how the different studies characterize the direction of species distributional shifts, we found that just ~12.1% (*n*=29) compare shifts simultaneously across all possible geographical directions (Hockey et al., 2011; Gillings et al., 2014; Taheri et al., 2016). That is, they generally investigate the species range changes across the expected direction of climate change (typically temperature change) while ignoring comparison with distributional changes across alternative directions (Fig I. 2a & Fig I.2b). Of the 29 studies that examine distributional changes across multiple directions just four tested if observed distribution shifts could have arisen by chance by comparison with a suitable null model (Forero-Medina et al., 2011; Wolf et al., 2016; Boisvert-Marsh et al., 2019; Taheri et al., 2020). Analyses of species distributional shifts across multiple directions were mostly conducted with animals (n=25). Plants feature in just four assessments(Groom, 2013; Hanberry & Hansen, 2015; Fei et al., 2017; Rumpf et al., 2018). Unlike studies addressing distributional changes in a single dimension (e.g., latitude or altitude), studies examining range shifts in multiple directions typically found shifts to be idiosyncratic while being difficult to ascribe a clear direction of change (e.g., Tingley et al., 2012; Rowe et al., 2015; Santos et al., 2015).

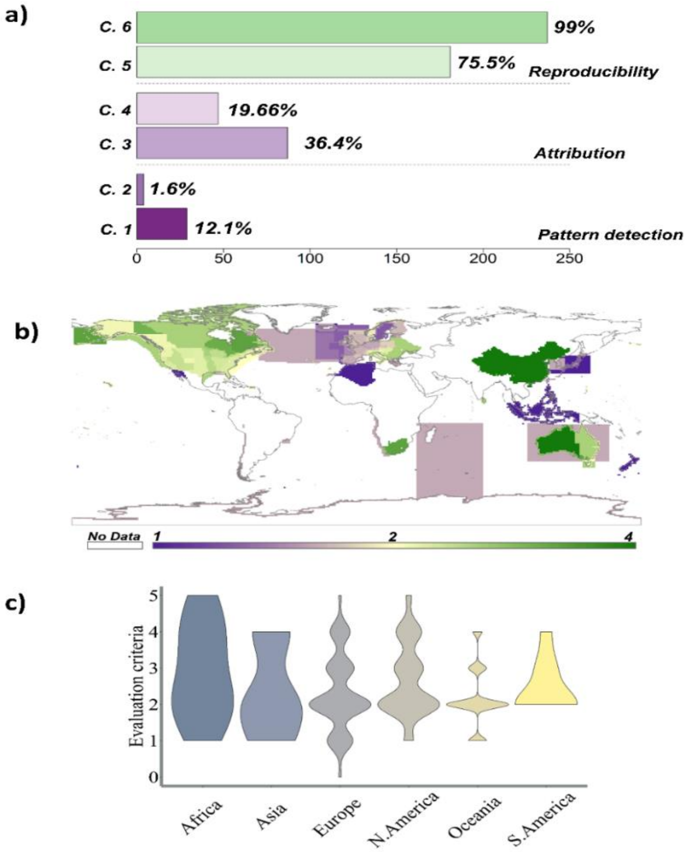

**Fig I.2**.The quality assessment in climate-related range shifts reports. a) The proportion of reports for six sub-criteria. The plot shows the proportion of each studies met each criterion. (C.1&C.2 Pattern detection, C.3&C.4 Attribution, and C.5&C.6 Reproducibility. b) Assessed quality of the reports of species redistribution under climate change across marine and terrestrial ecosystems. Shows the geographical distribution of studies investigating climate change effects on species distributions ranked by the overall (median) benchmark score achieved through summation of individual ranks in the three evaluation criteria. Values in the map range from 1 (only one of the evaluation sub-criteria met) to 4 (four of the evaluation sub-criteria met). Higher scores are colored green and lower scores are colored violet. c) Sum of the evaluation sub-criteria in each continent. Shows the number of evaluation sub-criteria met by each study across continents.

When investigating links between species distributions and climate change, ~59% (*n*=142) of the studies explicitly examine how temperature change covaries with species distributional changes. However, most studies disregard other environmental drivers, such as precipitation change, land-use change, or the interactions among them. Of the reviewed studies investigating causes of distribution shifts other than temperature change (36.4%; n=87), only 19.66% (n=47) have tested alternative causal factors on equal footing (Fig I.2a). Complex interactions among temperature and precipitation change, and species-specific tolerances intervening on species responses to climate changes, were examined in a few studies so far (Pinsky et al., 2013; VanDerWal et al., 2013).

When examining the reproducibility of studies, we found that ~25.5% (n=59) did not report data at the individual species level; a requirement for full reanalysis and replication of the studies (Fig I.2a).

The degree to which studies met our criteria also varied among regions: Australia, northern Europe, and a few studies in North America were generally more proficient (Fig I.2b & 2c). For example, among 40 papers that received score= 4 in our criteria scoring, 42.5 % (n=17) are in Europe and 37.5% (n=15) in North America. In total only six studies out of 240 received score = 5, in which two of them are in Europe, three of them in North America and one in Africa. Great Britain, although with the highest number of species distributional change studies (n=37), had an average (median) of just two sub-criteria met. China with three studies reviewed averaged 4 sub-criteria met, (Wu, 2015, 2016; Wu & Shi, 2016), all reporting heterogeneous and diverse responses of species to climate change (Fig I.2b & 2c).

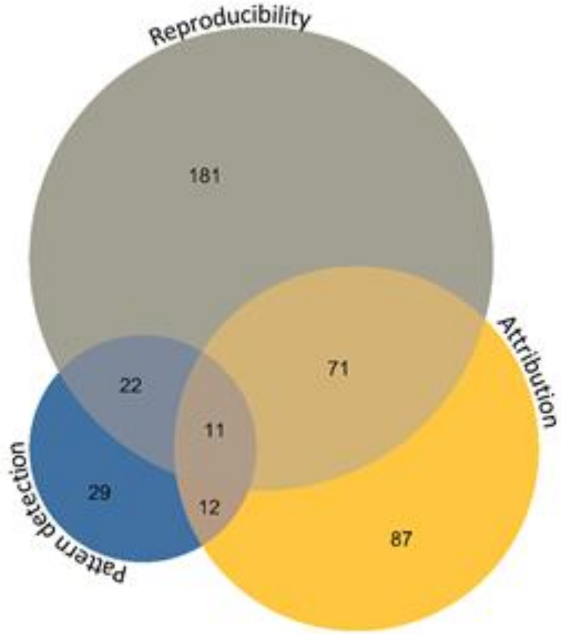

**Fig I.3.** Cross-examination of the sub-criteria used to evaluate reports of species redistribution under climate change. Shows the multiple overlapping among the three main criteria. Each circle corresponds to one of the main evaluation criteria. The size of the circles represents the number of reports met each main criterion (pattern detection, causality and reproducibility). The reuleaux triangle in the centre shows the intersection between three circles and it means only 4.5% (n=11) of studies met these three main criteria.

Overall, studies performed poorly against the three criteria (six sub-criteria) utilized (see box 11). Of the 240 papers reviewed, only 11 (4.5%) met the three criteria, i.e., detected changes in all possible directions, considered at least one other causal factor rather than temperature, and presented the results for individual species meeting all the three main criteria (Fig. I.3). Just 16.6% (*n*=40) met 4 sub-criteria, and only 2.5% (*n*=6) met 5 sub-criteria (e.g., Hockey et al., 2011; Wu, 2016).

In general, studies conducted for terrestrial ecosystems achieved greater performance according to the sub-criteria used (FigI.3b), although the sample size of studies in terrestrial ecosystems (*n*=193; 80.4%) is much larger than in marine ones (*n*=47).

We analyzed how the different aspects reflecting the quality of studies evolved through time given the criteria. We found that studies' performances had a tendency to increase across all criteria (Fig I.5). For example, among studies that measured multi-directionality of range shifts (*n*=29), 26 were published from 2011 onwards. Likewise, in this period, 60 studies out of 87 investigated multiple causal factors, while 116 out of 181 met our criteria for reproducibility.

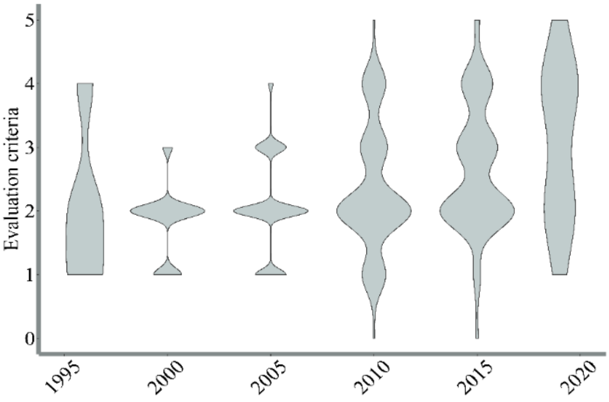

**Fig I.4.** Distribution of studies by evaluation sub-criteria over time. Shows a general trend of improvement of reports of climate-related range shifts over time across six sub-criteria. Higher values in y-axis means that more of the established evaluation criteria were met.

# Discussion

Species adapt to changes in climate by moving to more suitable locations (M. Araújo & Rahbek, 2006). Alternatively, some species might be able to persist throughout their known distributions due to phenotypic plasticity or adaptive genetic modification (Valladares et al., 2014; King et al., 2018). When neither of these options are available, species perish (Urban, 2015). The combined adaptive responses of species to climate change leads to changes in species ranges. Detecting changes using fragmented samples of data and identifying potential causes for those changes is particular challenging.

There are considerable uncertainties regarding the speed of distributional shifts (Svenning & Skov, 2004; M. B. Araújo & Pearson, 2005; García-Valdés et al., 2013), particularly along rear (contracting) edges(Wilson et al., 2005; Anderson et al., 2009), the accelerating or mitigating effects of biotic interactions(Callaway et al., 2002; Hughes, 2012), the capacity to adapt *in situ* associated with expressions of phenotypic plasticity(Valladares et al., 2014; King et al., 2018) or genetic modification(Franks & Hoffmann, 2012), and the effects of interactions among multiple climate drivers of change (Yalcin & Leroux, 2018). The tolerances of species to climate extremes are generally inferred with statistical approaches(Diniz-Filho et al., 2009; Garcia et al., 2012; Dullinger et al., 2012). However, circumstantial evidence suggests that inferred tolerances are narrower than real ones(M. B. Araújo et al., 2013; Herrando-Pérez et al., 2019). Combined, these biological and environmental effects can truncate the pace and direction of biological responses to climate change. Delayed responses are common (Essl et al., 2015), resilience to changes(Bernhardt & Leslie, 2013) has been observed, and the unknown consequences of novel climates are hard to anticipate (Pearson et al., 2006).

Additionally, current estimates of climate change effects on species distributions are severely hampered by geographic and taxonomic biases in the underlying data (Fig I.1) (see also Lenoir & Svenning, 2014) . Most data come from species-poor, mostly temperate, regions. In sharp contrast, the tropics hosting the vast majority the planet's biological diversity(Brown, 2014) scarcely have any study assessing climate change effects on species. A range of factors affects the availability of biodiversity-related information. The knowledge gap in tropics, for example, is related to insufficient funding, inadequate infrastructure, and scarce local expertise for data collection and identification, inaccessibility to research sites due to the political upheaval, and difficulties in getting data published or public (Collen et al., 2008). In addition, geopolitics (Trimble & van Aarde, 2012), regional democracy (Rydén et al., 2020), socio-economic, history, culture, scientific interest (Amano et al., 2016) and unwillingness of sharing the data, play an important role in biodiversity data collections and publishing bias.

While the impact of climate change on the future of biodiversity has been assessed for a wide range of taxonomic groups, the total number of empirical studies remains relatively low. One important reason for this is the lack of replicable historical surveys (but see (Morueta-Holme et al., 2015)) that limit the reliability of the assessed empirical relationships between species distributional changes and environmental changes (Hortal et al., 2008).

Studied clades also represent an extremely small fraction of the world's life forms: insects, by far the most specious group in the world, are almost not covered by assessments, and most studies are based on trees and vertebrates with 23% conducted on birds alone. Any conclusion drawn from existing data is thereby regional, taxonomically biased, and hardly transferable globally. Possible generalizations are, therefore, limited.

Adding to limitations of the data, we found that most studies underperform on the methodological standards of analysis. These are, however, more easily circumvented than the limitations of data. To ascertain if a distributional shift occurs in response to a given environmental driver, one needs to assess not just changes along the expected gradient but also along alternative gradients(Taheri et al., 2016). That is, if species are expected to change along a south to north gradient, for example, one needs to measure if the changes along latitude are significantly different from the changes along longitude. If not, it will be difficult to ascertain that changes are not a consequence of natural population dynamics of range expansion and contraction (Bradshaw et al., 2014). Even when distributional changes are examined across multiple directions, one might still ask if observed patterns could not have arisen by chance given geometrical constrains for dispersal or alternative environmental driver dynamics (Taheri et al., 2020). Addressing these questions requires the use of null models of distributional change, but although null models have made their way into ecology (Gotelli & Graves, 1996; Colwell et al., 2004) and biogeography(Hubbell, 2001), they are still hard to find in studies of climate change effects on biodiversity.

That correlation does not imply causation is well known. Nevertheless, when a good mechanistic hypothesis exists linking a pattern and the potential underlying mechanisms, and when expected relationships are observed repeatedly across different regions and times, accumulation of evidence can be interpreted as supporting hypothesized causal links between pattern and mechanism (M. B. Araújo et al., 2019) This is the logic linking elevation and latitudinal shifts with climate change: as temperature increases, higher latitudes and elevations are expected to warm, hence receiving more warm tolerant species while losing cold tolerant ones. Such is an observation dating as far as the classic observations of Alexander von Humboldt in the Chimborazo Mountain of Ecuador(Humboldt, 1838; Morueta-Holme et al., 2015). However, climatic gradients do not always follow geographical gradients linearly(Tingley et al., 2012), and most often there are feedbacks between temperature and other climatic variables (e.g., humidity and wind) that further affect the expected relationship between temperature and geographic gradients(Rapacciuolo et al., 2014). Seeking to attribute climate change to a given distributional shift is thus better achieved by relating species range changes with climate variables instead of geographical proxies, such as latitude and elevation. This point has been made several times for studies examining diversity gradients along elevation gradients(Körner, 2007) and latitude(Hawkins & Felizola Diniz-Filho, 2004) but, as our review shows, it has not been fully appreciated and integrated in assessments of climate change effects on biodiversity.

Additionally, even when climate change variables are used, instead of geographical proxies, to examine relationships with species distributional shifts, there are occasions when distributional shifts respond not just to climate but to other environmental changes, such as spread of disease (Hof et al., 2011) or land use change (Ameztegui et al., 2016; Yalcin & Leroux, 2018; Guo et al., 2018). Attributing a mechanism to an observed pattern thus benefits from examination of multiple alternative hypotheses on equal footing. Nevertheless, multimodal inference(Sirami et al., 2017) was found to be extremely rare in the reviewed literature.

Finally, a critical feature of science-based assessments is the ability to reproduce and build upon each other’s published results. Unfortunately, many findings cannot be reproduced. Our review reveals, ~25 % of the reports on distributional changes under climate change do not provide full access to the data and detailed results. Reproducibility contains several elements such as selective reporting, methods and availability of codes, statistical power, experimental design and availability of raw data. In this review, we focused on selective reporting. However, we notice that considering other factors of reproducibility could dramatically affect our assessment of published studies. Recently, a study (Baker, 2016) carried out by 1500 scientists from different disciplines (e.g., chemistry, physics, medicine and biology) showed that most of the scientific articles are not fully reproducible;, our review corroborates their findings in the subfield of climate change ecology and biogeography.

Moving forward in the capacity to assess the where, when, and why of climate change effects on biodiversity is crucial to guide the timing and magnitude of human adaptation strategies for biodiversity. In our scan of the literature, we asked very simple questions that enable establishing inferences about the quality of the underlying data and methods. We demonstrate that substantial improvements should be considered in assessments. Most of them do not require reinventing concepts or methods. Questions about the need for null models to discriminate expected directional patterns from stochastic (or more complex) ones(Harvey et al., 1983; Gotelli & Graves, 1996), or the disadvantages of using indirect proxies as opposed to direct variables with proven mechanistic links to the patterns (Hawkins & Felizola Diniz-Filho, 2004; Körner, 2007), are well established in the ecological literature. Somehow, these debates and the associated recommendations have not percolated through studies examining climate change effects on species distributions.

Our study provides a hint of the best-practice standards needed for assessments of climate change effects on a specific facet of biodiversity change: species range change. Other biodiversity change facets, such as local patterns of colonization and extinction, or abundance changes, or changes in community composition are not covered by our analysis, partly because very few of such studies exist across multiple species. Future investigations should seek to expand the facets of biodiversity change considered in quality assessments and strive to build consensus on the standards required to increase the strength of evidence of climate change impacts on biodiversity while developing detailed guidelines to help increasing the robustness, transparency, and reproducibility of the assessments.

# Methods and Materials

## Literature review

We identified papers by screening published reviews(Lenoir & Svenning, 2014) and meta-analyses(Parmesan, 2006; I.-C. Chen et al., 2011), and by searching the primary literature using engines such as Google Scholar, ISI Web of Science, Scopus, Wiley Online Library. We used a combination of the following keywords in our search: “climate change” or “climate warming”, and “range” or “distribution”, and “poleward/ northward shift” or “upslope/ altitudinal shift” or expansion/contraction (Supplementary material Fig A 1.1). We then filtered the records by using some inclusion and exclusion criteria. These criteria comprised references that assessed distributional changes based on species occurrence data over at least two historical periods. Since our focus was on the empirically observed distributional shifts, we excluded papers that used abundance or richness data alone or those that used modelling and/or predictions to quantify “future” or “potential” changes. Our search criteria provided a set of 240 publications.

### Data mining

Following the literature search, we extracted the relevant data to be structured in a suitable database (Table S1). For each publication, we recorded the following information: (i) study year; (ii) spatial scale (e.g., local, regional, and continental); (iii) geographic region as reported in the study; (iv) ecosystem type (terrestrial versus marine); (v) climate zone; (vi) magnitude and direction of distributional shifts; (iv) total number of taxa and their identity (taxonomic group, species names); (vi) time period; (vii); and (viii) the general methodology used by the study (Supplementary material Table S1).

In the database, a unique code was assigned to each article reviewed and its geographic location was also recorded. In order to effectively visualize the spatial coverage of the reports, we digitized the geographical boundaries of all the studies reviewed either as a set of spatial polygons or points depending on the geographical extent of the study. We then used a regular two-degree (~2×69 miles) grid cells covering the world’s land and sea areas in ArcMap software (version 10.1) to aggregate the digitized points and polygons into the grid cells and quantify the frequency of the studies at each cell.

We used the Köppen climate classification(Peel et al., 2007) to group the studies into the climate zones. In addition, we aggregated the spatial boundaries of the studies within the five major climatic zones defined by the Köppen climate classification based on seasonal temperature and precipitation patterns. The five climatic zones are (i) tropical, (ii) dry, (iii) temperate, (iv) continental/cold, and (v) polar.

In order to sort the taxonomic coverage of the data used in the studies, we first extracted the number of species and their scientific names for the given taxonomic group in each article (Supplementary Material Table S3). We added the names of species to the database and after removing duplicate records we calculated the proportion of species considered in studies (Table A2.1).

### Assessment criteria

The assessment of published studies was made following a simple set of criteria as described in Box 1. For pattern detection, we focused on the methodological aspects of the studies. We explored how the species distributional shifts were measured. Specifically, we asked if distribution shifts were analysed across all potential directions (e.g., latitude, longitude, and elevation), and whether the null expectation regarding distributional changes (likelihood of changes derived from patterns shifted by chance due to internal variability) was determined. Therefore, scientific publications that assessed distributional shifts within all the possible directions, rather than only along a single elevation or latitudinal axis, and also compared the results against the patterns expected by chance (null distribution), received the maximum score for the pattern detection group benchmark.

For attribution, we asked if studies examined potential causal links between observed distributional changes and environmental predictors (e.g., climate, precipitation, land use). We carefully reviewed the studies methods sections to assess how (if at all) they attributed observed shifts in species distributions to climate change and what approaches were used to perform the task. The papers that investigated multiple alternative causal factors on equal footing, rather than simply examining patterns against a single predictor (e.g., temperature), received maximum score for the attribution criteria.

For reproducibility, we examined the results sections of the studies. A study received the full score for this group if the results were available for each individual species analysed and if the divergence responses among species were fairly reported.

# **II CHAPTER.** DISCRIMINATING CLIMATE, LAND-COVER AND RANDOM EFFECTS ON SPECIES RANGE DYNAMICS

Shirin Taheri1; David García-Callejas; Miguel B. Araújo

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# Discriminating climate, land-cover and random effects on species range dynamics

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## Abstract

Species are reportedly shifting their distributions poleward and upward in several parts of the world in response to climate change. The extent to which other factors might play a role driving these changes is still unclear. Land-cover change is a major cause of distributional changes, but it cannot be discarded that distributional dynamics might be at times caused by other mechanisms (e.g., dispersal, ecological drift). Using observed changes in the distribution of 82 breeding birds in Great Britain between three time periods 1968-72 ($t_1$), 1988-91 ($t_2$) and 2007-2011 ($t_3$), we examine whether observed bird range shifts between $t_1$-$t_2$ and $t_1$-$t_3$ are best explained by climate change or land-cover change, or whether they are not distinguishable from what would be expected by chance. We found that range shifts across the rear edge of northerly-distributed species in Great Britain are best explained by climate change, while shifts across the leading edge of southerly-distributed species are best explained by changes in land-cover. In contrast, at the northern and southern edges of Great Britain, range dynamics could not be distinguished from that expected by chance. The latter observation could be a consequence of boundary effects limiting the direction and magnitude of range changes, stochastic demographic mechanisms neither associated with climate nor land cover change, or with complex interactions among factors. Our results reinforce the view that comprehensive assessments of climate change effects on species range shifts need to examine alternative drivers of change on equal footing and that null models can help assess whether observed patterns could have arisen by chance alone.

# Introduction

Assessments of climate change effects on biogeography are largely driven by observational studies relating changes in species distributional shifts with geographic or climatic gradients (I.-C. Chen et al., 2011; Pecl et al., 2017). When distributional shifts match expected gradients, it is assumed that climate change is the likely driver of such shifts. Besides issues with data quality, which often pervade under-replicated studies across spatial and temporal dimensions, there are two potential problems with such an approach. The first is one of pattern detection. How can one be sure that the observed patterns would not have arisen by chance? The second is one of attribution. How can one be sure that the hypothesized drivers are the ones driving the observed pattern?

These are classical problems of inference based on correlations, and no easy solutions exist. Nevertheless, problems of pattern detection can often be handled within a null modelling framework that seeks to assess whether observed patterns in any given response variable (e.g., a species distributional change) could have arisen by chance (Gotelli & Graves, 1996). Null models are commonly used for testing ecological theory, but they are notoriously uncommon in studies assessing species distributional shifts and their underlying drivers (Taheri et al., 2021). Such models typically involve the use of randomized ecological data subject to sets of constraints and are designed to produce a pattern expected in the absence of a particular ecological mechanism. The generated (random) pattern can be compared with the real pattern of interest (Gotelli & McGill, 2006). Conceptually, null models help discerning patterns in the data but they do not necessarily reveal the underlying causal mechanisms (Peres-Neto et al., 2001).

Problems of attribution are also inherent to the use of correlations for inferring causation. Confidence in the inferences with correlative methods comes from accumulation of evidence and, ideally, from accumulation of evidence arising from multiple (and diverse) sources (e.g., Araújo et al. 2019). For any particular analysis, the problem is particularly challenging when multiple candidate predictors covary, which limits the ability to discern the variables truly driving observed patterns or, more subtly, how they interact to conform the observed pattern (Dormann, 2007). Testing model inferences requires independent replication but empirical data in many ecological problems is notoriously under-replicated (Lemoine et al., 2016). One approach to deal with uncertainty brought by covarying candidate predictors is to compare, on equal footing, inferences made with alternative sets of predictors (Burnham & Anderson, 1998). While such an approach is familiar in ecology (e.g, Araújo et al., 2008; Eglington & Pearce-Higgins, 2012; Rangel et al., 2018), it is seldom used for studying mechanisms driving observed species distributional dynamics (e.g, Rich & Currie, 2018). For example, a recent study demonstrated that previous analysis examining climate change signals on the distributional shift of British birds (Thomas & Lennon, 1999), overestimated these signals by failing to examine distributional changes across multiple dimensions (Taheri et al., 2016).

The matter of fact is that shifts in range edges toward higher latitude or elevation are often interpreted as a response of species to warming climate (e.g., Chen et al., 2011; Hickling et al., 2006; Parmesan et al., 1999). However, variation in magnitude and direction of such range shifts suggests that climate, particularly temperature, might not be the sole driver (e.g., Fei et al., 2017; Taheri et al., 2016). Shifts in geographic distributions of species may also reflect natural population dynamics (Bradshaw et al., 2014), or complex interactions with other factors such as human-mediated land-use change (e.g., Guo, Lenoir, & Bonebrake, 2018; Lehikoinen et al., 2013), dispersal limitations (Anderson et al., 2009) competition (Marion & Bergerot, 2018), biological invasions (Sax & Gaines, 2008), disease (Hof et al., 2011) and interactions among several factors (e.g., Vicente et al., 2019).

Understanding range dynamics and their underlying causes thus requires more sophisticated analysis than is typically performed. In this study, we illustrate these issues by examination of historical range dynamics among 82 bird species in Great Britain against three alternative models: climate change model, assuming that distributions changed following climate changes; land-cover change model, assuming that species distributions changed following land-cover changes; and a null model that, while keeping the same quantities of observed distributional changes (expansions and contractions), randomized the direction of the changes. Because drivers of species range shifts are unlikely to be equally important across different sections of species ranges and following previous studies of range shifts in Great Britain (e.g., Hickling et al., 2006; Thomas & Lennon, 1999), we independently examine four sections of species distributions: leading and rear edges of the southern and northernmost edges of southerly and northerly-distributed species (Fig I.1e).

# Methods and materials

## Species data

We used species distributional data from three Atlas of breeding Bird surveys compiled for Great Britain, providing presence and absence records at 10 × 10 km spatial resolution. The first atlas covered the period of 1968-72 (t1) (Sharrock, 1976). The second covered the period of 1988-91 (t2) (Gibbons et al., 1993). The third included records from 2007-11 (t3) (Balmer et al., 2013). The Atlases used the Ordnance Survey National Grid as a means of identifying location of bird records. This standard inventory-type surveys aimed at generating ‘hectad’ (10 × 10 km) resolution distribution maps, and incorporated fixed-effort data using timed visits to a sample of ‘tetrads’ (2 × 2 km squares) in each hectads (Gillings et al., 2019).

We digitized the distribution data from online-published sources (https://www.bto.org/). We excluded marine species and restricted-range species with less than twenty records in the first atlas data since small range changes in restricted range species can have a great relative effect even if driven by stochastic factors. We also excluded wide-ranging species with more than 2000 records (ubiquitous species) in the first atlas (t1) (Britain includes 2280 10-km grid cells), since the capacity to shift ranges biased towards range reduction. Using these criteria, we selected 82 species for analysis, involving species range comparisons between t1 and t2 (twenty years) and t1 and t3 (forty years).

### Climate

We used a time series of changes in maximum and minimum temperatures and annual precipitation at a spatial resolution of 0.5 degrees from the updated version of the Climate Research Unit's database (http://www.cru.uea.ac.uk). The baseline covered the period of 1958-2011, and then we sliced climate data for a 15 years interval before the last census in each period. The climate slices are as follows: For the t1 period, we used climate time series from 1958 to 1972; for t2, from 1977 to 1991; and for t3, from 1997 to 2011. We used fifteen years of climate data for each atlas on the assumption that species' ranges respond to the long-term average of climate conditions.

The climatic variables were processed using R BioCalc function (Ramirez 2009). They included Maximum Temperature of Warmest Month, Minimum Temperature of Coldest Month, and Annual Precipitation. Our choice of variables reflects those known to impose general constraints on bird distributions in Europe (Lennon et al., 2000; Whittaker et al., 2007). We then downscaled climate data using Inverse Distance Weighting (IDW) following (Shepard, 1968) in raster package R (Hijmans et al., 2018). Inverse distance weighting (IDW) is a method of interpolation that estimates cell values by averaging the values of sample data points in the neighbourhood of each processing cell. The closer a point is to the centre of the cell being estimated, the more influence, or weight it has in the averaging process (Zhou & Zhang, 2014). The output cell size and other parameters of the new raster layers were matched to the 10 * 10 km of bird's atlas dataset.

To examine the climate-based prediction, we developed ensemble species distribution models using the sdm package in R (Naimi & Araújo, 2016). We modelled each species presence/absence as a function of the three climate variables. We ran five different algorithms for modelling the presence/absence of birds using an ensemble modelling framework (Araújo & New 2007): generalized linear models (GLM; McCullagh & Nelder, 1989), generalized additive models (GAM; Hastie & Tibshirani, 1990), random forest (RF; Breiman, 2001), mixed effect modelling (FDA; Hastie et al., 1994), boosted regression tree (BRT; Friedman, 2001) Fig 6a). In order to avoid biases to the parameter estimation, we used a bootstrapping method (Fielding & Bell, 1997; Hastie et al., 2009) with 100 random replication for each species and modelling technique. Bootstrapping repeats a sampling with replacement, each time a sample with equal size as the original data is drawn and used for training data. The observations that are not selected are used for the evaluation at each run. Then we generated a consensus model, using weighted average probability for each species, where weights were obtained from the AUC in evaluation data (Marmion et al., 2009; Garcia et al., 2012).

To assess habitat suitability based on climate constraints, we converted probabilistic output to presence/absence using one of the recommended threshold techniques: Max (Sensitivity +Specificity) (Liu et al., 2005). Values above or equal to the threshold are classified as predicted species presences, while values below the threshold are classified as predicted absences. When the presence/absence map was provided for each species, we measured the range shift and compared the results of climate related range shifts with observed range shifts.

### Land cover

We used land-cover change estimates from the Laboratory of Geo-information Sciences and Remote Sensing at the University of Wageningen (HILDA version 2.0). The HILDA dataset is available at a 1km spatial resolution from

1900-2010 for the whole Europe (Fuchs et al., 2012, 2015). The temporal resolution of the dataset is decadal (10 years) and contains six land-cover classes:

1- Settlement (incl. green urban areas);
2- Cropland (incl. orchards and agroforestry);
3- Forest (incl. transitional shrub and woodlands, tree nurseries, reforested areas for forestry purposes);
4- Grassland (incl. natural grassland, wetlands, pasture and Mediterranean shrub vegetation);
5- Other land (incl. glaciers, sparsely vegetated areas, beaches, bare soil);
6- Water (incl. water bodies, sea, streams).

We considered three decadal land-cover survey periods approximately matching species atlas surveys: 1960; 1980; and 2000. The proportion of individual land-cover classes present within each 10 km Bird Atlas grid cell (Fig 6b) was then calculated. In order to determine the signal of land-cover changes on species range shifts, we run the same species modelling techniques used for climate but with land-cover variables instead (Thuiller et al., 2004). Specifically, we modelled each species presence/absence as a function of the six land-cover predictors. Following the procedure used with climate variables, we ran five different algorithms to model the presence and absence of bird species within an ensemble-modelling framework. We used the land-cover predictors for the 1960s (t1) as baseline. Then, we projected distributions using land-cover predictors in 1980s (1960 vs. 1980, Twenty years) and 2000s (1960 vs. 2000, Forty years). Like with the climate models, we generated 100 random replication using bootstrapping (sampling with replacement) for each species and modelling technique. We used AUC in evaluation data, to obtain the probability of distribution for each species and used the same threshold method implemented with the climate model to convert the probabilities generated from the land-cover model into presence and absences.

To address the link between the magnitude of the land-cover change and species range shifts, we first selected all persistence cells (cells where species remained present from the first to the second survey (Presence in t1 ∩ Presence in t2 or t3). Then, we treated all persistence cells as static, while randomizing newly occupied cells in t2 or t3 within the potential cells that had a high probability of occurrence as projected by the ensemble models using the land-cover predictors. Here, the constrained randomization ensures that each novel presence has an equal chance of occupying any of the suitable sites predicted by the land-cover model. In order to estimate the variability of the results, we replicate the randomization process 100 times for each species. We used the average of these replications to measure the range shifts constrained by land-cover and compared the results with observed range shifts.

### Null model

We developed a patch-occupancy null model to infer expected range shifts in the absence of climate change or land-cover change but with the geographical constraints imposed by the geometry of Great Britain, while maintaining the observed rates of expansion or contraction of the 82 species in the intervals t1-t2 and t1-t3. In a given interval, the model computes the null expected range shift of each species as follows.

First, denote as Pt1 the set of cells in which the species is present at the first atlas. Likewise, Pt2 is the set of cells with presence of the species in the second census (either time t1 or t2). Further, denote as Ps the set of cells in which the species persists from the first to the second census, and with Pc the set of cells newly colonized by the species in the second census. Thus, the number of occupied cells in the second census is simply |Pt2| = |Ps| + |Pc| where the double bars indicate the cardinality of a set, i.e., the number of elements it contains. If the species has expanded its distribution, $|Pt2| > |Pt1|$, which implies $|Pc| > 0$ but allows for $|Ps|$ to reach 0, in the limit case in which a species changes its whole range between censuses. On the other hand, if the species has suffered a contraction between censuses, it means $|Pt2| < |Pt1|$, this case implying $|Ps| < |Pt1|$.

The null model keeps the number of persisting occurrences and colonized cells of each species fixed, and simply distributes stochastically these quantities ($|Ps|$ and $|Pc|$) across the appropriate sets of cells. In particular, for each realization of the model for a given species, the first step is to assign the cells in which the species persist. Since we assume that all cells are equivalent, we expect species to persist with equal probability in any of the cells occupied in the first census. Therefore, we randomize the number of persisting cells, $|Ps|$, among the set of occupied cells at T1, Pt1. Using set operations, the randomized $Ps \subseteq Pt1$ (panel i) of Fig 1c). The second step is assigning the colonized cells, Pc. Again, as we assume no other constraints, any cell of the whole territory can be assigned a presence. Thus, if T is the set of cells of the whole territory, in each realization we randomize $Pc \subseteq T$ (panel ii) of Fig 1c). This approach accounts for expansions and contractions in the number of cells with persistent occurrences ($t1 = 0$, $t2 = 1$) or colonized cells ($t1=0$, $t2=1$), thus including the whole variability of range shifts observed. In this study, we generated 1000 draws of the null model for each one of the 82-bird species considered, totalizing 82000 null model distributions. The final analysis of range shifts was carried out with averaged shifts across these 1000 replicates for each species.

## Analysis of range shifts

To relate observed species range shifts to our three alternative modelled shifts (constrained by climate, by land-cover, or random dynamics), and following Thomas and Lennon (1999), we first split species into northerly- and southerly-distributed depending on whether their distributional core lies to the north or to the south of the mean position of the all 100 km2 grid cells in Great Britain, respectively (Fig 1e; Table S4). Overall, we obtained 47 and 35 southerly and northerly-distributed species, respectively.

We then examined range changes along leading and rear edges. Shifts in range margins between two atlases were calculated as the mean distance of 20 most marginal records in the southern and northern margins in t2 or t3 minus t1; positive values indicate a move toward the boundary (expansion) and negative values indicate a move toward the core of the distribution (contraction) Figure 1d). Then we provided Presence/Absence map for three alternative models (climate, land-cover, null) and compared shifts at the leading and rear edge with observed data using the Wilcoxon signed-rank test.

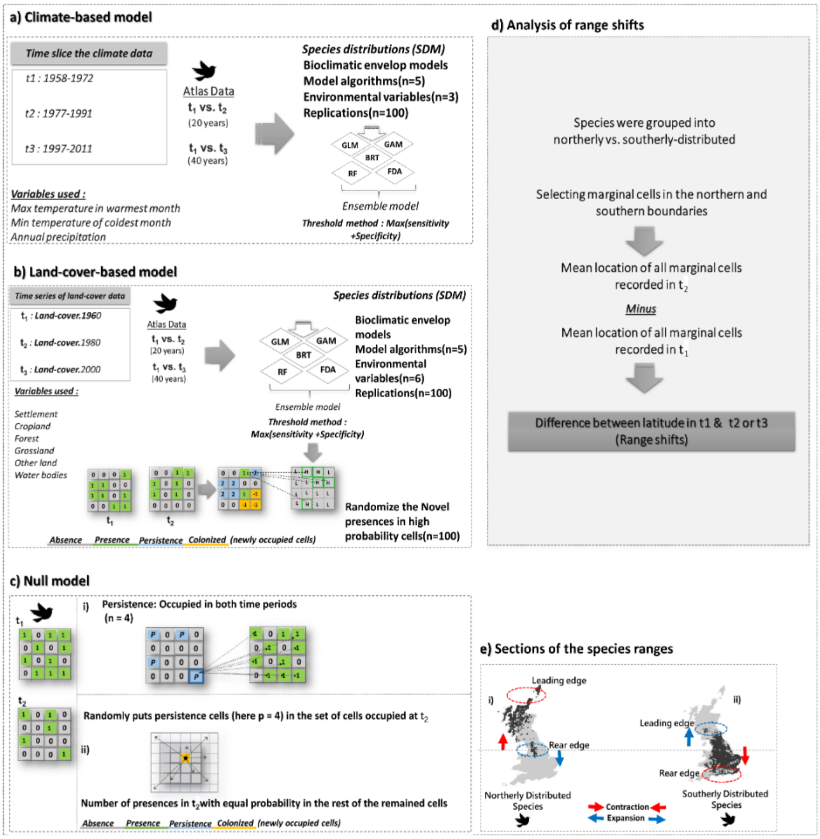

**Fig II.1**.Methodological framework. a) Climate model, (b) Land-cover model, c) Null model, d) Analysis of range shifts. Presence/Absence map was generated for each species based on the three alternative models. The pattern of range shifts was compared with the observed data using the Wilcoxon signed-rank test. e) Sections of the species ranges. Shows the different sections of the distributions. Leading and rear edges of southerly-distributed species (n=47), and rear and leading edge of northerly-distributed species (n=35).

# Results

Comparison of observed range shifts with projections arising from the three alternative models revealed that determinants of species range shifts were seemingly variable across each one of the four predefined sections of the range (Fig II.1 e).

At both the southern and northern tips of Great Britain (i.e., the rear edge of southerly-distributed species and the leading edge of northerly distributed-species), observed range shifts were no different from expected by chance; this being true for both the $t_1$ vs $t_2$ and $t_1$ vs $t_3$ comparisons (Fig II.2 c, d and c, d). Observed trends were also no different than expected by chance with respect to both the climate and land cover change models, making it difficult to attribute observed changes to any specific driver.

At the rear edge of northern distribution, observed range shifts, were inconsistent with range changes obtained with the null model (Wilcoxon signed-rank test $P<0.001$; Figure 2b and Figure 3b) as well as with the land cover model ($P<0.01$ and $P<0.001$ for the 20 years and 40 years comparison respectively; Figure 2b and Figure 3b), which predicted a shift of opposite direction as observed. Observed range shifts were, in turn, consistent with that estimated with the climate model (Figure 2b and Figure 3b). Such consistency between observation and modelled shifts can be interpreted as indicating the existence of a climate change signal in species distributional dynamics in this geographical section of the range.

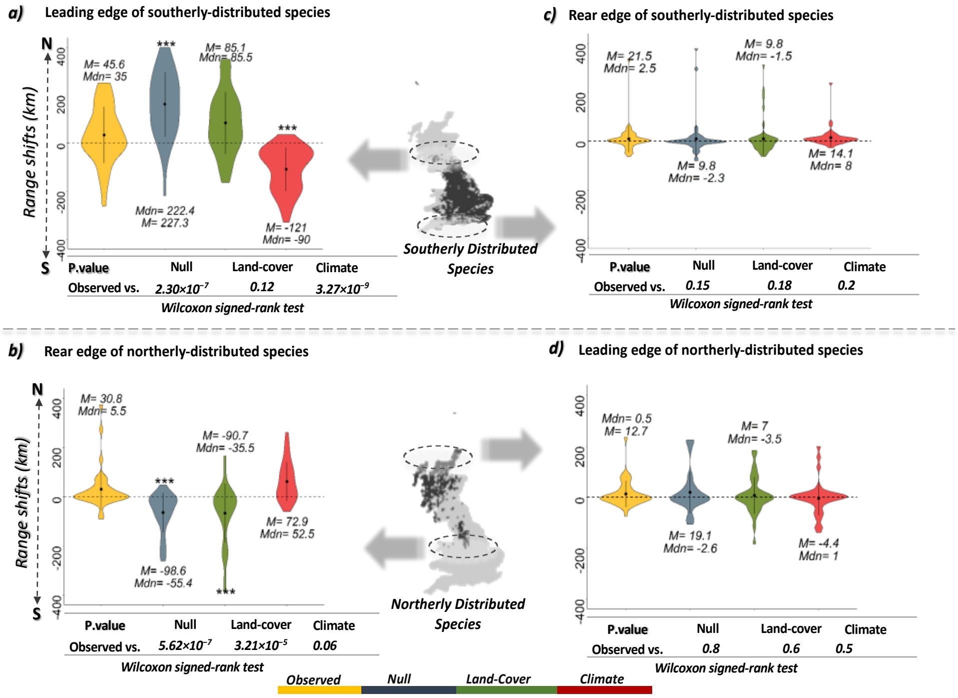

**Fig II.2**.Violin plots depicting the frequency distribution of range shifts between (1968-72 and 2007-11) among leading (a) and rear (c) edges of southerly distributed species (n=47), and rear (b) and leading edge (d) of northerly distributed species (n=35). The degree of mismatch between observed shifts (yellow) and range shifts predicted by the null model (blue), land cover model (green), and climate model (red). The black dots inside the violin plots show the median and the vertical line shows the deviation from the mean. *** and * indicate if there is any significant difference from observed shifts p < 10-3 and p < 0.05 respectively using (Wilcoxon sign rank test). Maps in the different sections of the distribution and are an example of leading and rear edges of southerly and northerly-distributed species.

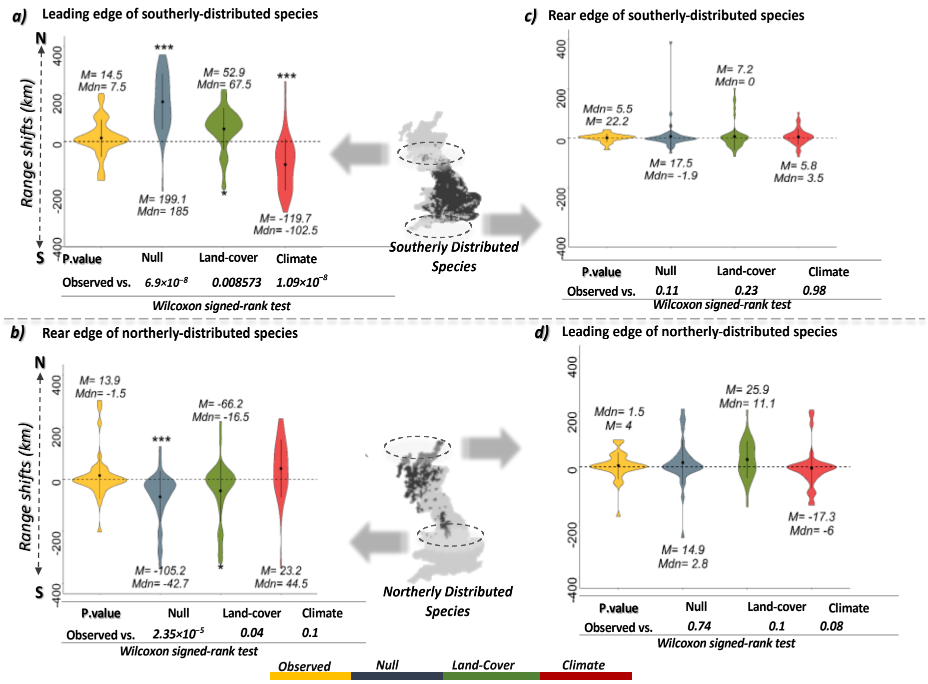

**Fig II.3.**Violin plots depicting the frequency distribution of range shifts between (1968-72 and 1988-91) among leading (a) and rear (c) edges of southerly distributed species (n=47), and rear (b) and leading edge (d) of northerly distributed species (n=35). The degree of mismatch between observed shifts (yellow) and range shifts predicted by the null model (blue), land cover model (green), and climate model (red). The black dots inside the violin plots show the median and the vertical line shows the deviation from the mean. *** and * indicate if there is any significant difference from observed shifts p < 10-3 and p < 0.05 respectively using (Wilcoxon sign rank test). Maps in the center show different sections of the distribution and are an example of leading and rear edges of southerly and northerly-distributed species.

More specifically, observed data showed a general tendency for northward shift with a mean of 14 km (median = -1.5) during the 20 years comparison and a mean of 30.8 km (median = 5.5) during the 40 years comparison. Climate models projected a northward range shift of greater magnitude with a mean of 23 Km (median= 44.5; Figure 2b) during the 20 years and a mean of ~72.9 km (median = 52.5; Figure 3b) during the 40 years.

At the leading edges of southerly-distributed species, range dynamics were again inconsistent with the null model (*P*<0.001; see Figure 2a and Figure 3a) and with the climate model projections (*P*<0.001; Figure 2a and Figure 3a), which predicted shifts of opposite direction as observed. The land land-cover model generated, in contrast, projections that were consistent with observed range shifts (Figure 2a and Figure 3a). Specifically, observed trends indicate a northward shift by average of 14.4 km (median = 7.5) during the 20 years and 45.6 km (median = 35) during the 40 years. The land-cover model inferred the same trend of northward expansion by 52.9 km (median= 67.5; Wilcoxon signed-rank test, *P* = 0.008 Figure 2a) during the 20 years and 85 km during the 40 years (median= 86.5; Wilcoxon signed-rank test, *P* = 0.1; Figure 3a) respectively.

# Discussion

We show that different mechanisms are likely implicated in shaping bird range dynamics across Great Britain and that the importance of such mechanisms (e.g., climate change versus land cover change) varies across sections of species ranges. While rear edges of northerly-distributed species have shifted in a way consistent to projections from a climate driven model, shifts at the leading edge of southerly-distributed species, carry a stronger imprint of land-cover change. In contrast, shifts at the leading edges of northerly-distributed species and rear the edges of southerly-distributed species—that is, distributions at both the northern and southern tips of Great Britain--were no different from that expected by chance.

One question arising when interpreting range shifts in a geographically bounded area, such as Great Britain, is the extent to which the magnitude and direction of range changes are constrained by the geometry of the region (see

Gillings et al., 2014; Groom, 2013). For example, suppose that a species is distributed in the easternmost corner of the Island and that climate change would drive species to expand north. Since north of that region there is boundary with the sea, the species would be blocked from moving north having to first move west and then north. Such constraints could have played a role in species distributional dynamics at the leading margins of northerly-distributed species and rear margins of southerly-distributed species, where the northern and southern terrestrial boundary of Great Britain restricts movement. In addition to the shape of the boundary, there can be other natural boundaries (e.g., mountain ranges, rivers, fragmented habitats) that prevent dispersal and reduce the rate of species adaptation to climate change through shifting ranges.

Geometric constraints on the spatial distribution of species is not an entirely new topic (see Colwell & Lees, 2000). For example, Keith et al (2011) showed that physical barriers have restricted dispersal of pelagic larvae in the south coast of England. Another study showed that the absence of *Mecistogaster modesa* in south America is strongly related to physical barrier such as Andes mountain range and oceanic barriers (Amundrud et al., 2018).

Despite previous insights on geometrical constraints, only a few studies have compared observed species distributional changes with null models to discriminate between directional patterns of range change and non-directional ones (e.g., potentially arising from stochastic processes). One of such examples involves the use of Monte Carlo simulations to generate distributions of species across elevation under the null hypothesis (Forero-Medina et al., 2011). In that study, the authors found that by chance alone, 55 birds in Peruvian mountains could have moved on average ~40 m upward in elevation during 40 years.

Although a great deal of research on species range shifts has focused on climate change and its signals (e.g, Hanberry et al., 2011; Hickling et al., 2005; Parmesan et al., 1999; Thomas & Lennon, 1999) population declines have also been linked to agricultural intensification and fragmentation, fertilizer application, or pesticide use through time (Chamberlain et al., 2000; Eglington & Pearce-Higgins, 2012; Reino et al., 2018). There is also evidence that land-cover or agricultural practices can cause varying types of range shifts depending on behavioural and trophic characteristics of the species (e.g, Gaüzère et al., 2020; Reino et al., 2018). For example, *Spiza americana,* a grassland bird from North America, displayed northward expansions during 1960-1980 owing to changes in winter food supply associated with changing agricultural practices from rice growing to cattle raising (MacArthur, 1972).

In our study, we had no detailed information on agricultural practices at the cell level and analyses were based on patterns of change across six broad types of land-cover classes. Including more detailed information on agricultural practices can provide more reliable estimation of the magnitude of species range shifts under land-use (rather than coarse land cover) change. Our results are consistent with previous studies showing that expansions at leading edges of species ranges can arise as a consequence of land-cover change (Lima et al., 2007; Groom, 2013). In the Italian Alps, for example, the upward shifts of 21 bird species between 1982-2017 have been attributed to shrub and forest cover expansion (Bani et al., 2019), and range expansion among 10 out of 23 birds in the Czech Republic seems to be affected by habitat change (Reif et al., 2010).

We have considered the independent role of individual models (climate, land cover and null) by comparing their outputs against observed trends, on equal footing. However, global change drivers do not act independently from each other. Indeed, some recent studies detected these synergistic and antagonistic interactions between climate change and human disturbances or land-use change (e.g., Dainese et al., 2017; Elsen et al., 2020; Guo et al., 2018). Although a detailed analysis of the synergistic effects among different drivers is beyond the scope of this paper, we examined the presence of potential interactions between climate and land-cover change using an ANOVA framework and found significant interactions effects (Supplementary material). At the rear edge of northerly-distributed species, for example, maximum temperature interacts with forest loss and may be underlie northward shifts, while maximum temperature in interaction with forest gain covaries with southward shifts (Figure S2 c). Another example of interaction effect was between open-lands and minimum temperature at the leading edge of southerly-distributed species. The results show that minimum temperature interacts with open-lands loss and potentially drive species to move further to the north with higher magnitude (Figure S2 a, S3 a). Such post hoc analysis of the interactions among drivers of range change reveals that although we could successfully identify variation in the main drivers contributing to range shifts of birds in Great Britain, however the interaction among the independent variables should be also taken into account when possible.

To our knowledge, we provide the first empirical assessment of alternative mechanisms underlying range changes in different sections of the species ranges, on equal footing. Moving forward to assess the where and when of climate change effects on biodiversity is crucial to guide the timing and magnitude of human adaptation strategies for biodiversity. We highlight the substantial need for methods that are able to distinguish between directional and non-directional changes, thus being able to help tease apart distributional changes driven by natural population dynamics from changes driven by external forcing (climatic or non-climatic).

# III CHAPTER. *CLIMETRICS*: R PAKAGE TO QUANTIFY MULTIPLE DYNAMITIOS OF CLIMATE CHANGE

Shirin Taheri1; Babak Naimi; Miguel B. Araújo

Manuscript near submission to Ecography

# *Climetrics*: R package to quantify multiple dimensions of climate change

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Manuscript near submission to Ecography

## Abstract

Different dimensions of climate change affect biodiversity in different ways. To begin understanding such differences, one needs to explore different facets of climate change using convenient standard measurements (metrics). However, methods to quantify them are scattered and no tools currently exist to quantify alternative climate change metrics within a unified and standardized framework. To fill the gap, we developed "*climetrics"* which is an extensible and reproducible R package to spatially quantify and explore multiple dimensions of climate change. Six widely used metrics of climate change are implemented in the package including: 1) Standardized local anomalies; 2) Changes in probability of local climate extremes; 3) Change in area of analogous climates; 4) Novel climates; 5) Change in the distance to analogous climates; and 6) Climate change velocity. *climetrics* measures the velocity of climate change using three different algorithms; a) distanced-based

velocity ("*dVe*"); b) *threshold-based velocity ("ve");* and c) gradient-based velocity ("*gVe*"). The package also provides additional tools, e.g., to calculate monthly mean climate over a period of time; to quantify and map temporal trend (slope) of a given climate parameter at the pixel level; and to classify and map Koeppen-Geiger (KG) climate zones. The *climetrics* R package is linked to the *rts* package to efficiently handle raster time-series datasets. The functions in "*climetrics*" are designed to be user-friendly to less experienced R users, while being thoroughly commented upon to facilitate further customization by advanced users. The *climetrics* R package is a useful tool to explore the spatiotemporal patterns across multiple dimensions of climate change.

## Background

Climate is a multivariate phenomenon. Not only it involves different parameters, like temperature, precipitation and wind, but it also expresses itself at different geographical extent and temporal scales. Adequately capturing the wealth of climate change manifestations and the ways it interacts with the living systems requires that its multiple dimensions to appropriately be characterised through alternative, often orthogonal, metrics (Garcia et al., 2014).

Conceptually, the metrics of climate change can be quantified at the local (based on a single cell or pixel) or regional (that involves multiple cells) level (Garcia et al., 2014). The former has a temporal dimension, while the latter involves both spatial and temporal (i.e., spatiotemporal) dimensions. For example, the local metrics, such as anomalies (e.g., Araújo et al., 2008), standardized anomalies (e.g., Williams & Jackson, 2007), probability of extreme events (e.g., Jiménez et al., 2011), and changes in seasonality (e.g., Lane et al., 2012), characterize the magnitude of changes by quantifying how average or extreme values in the frequency distribution of climate change data series are altered in a given locality (a cell or pixel in a raster layer) over time. In turn, regional metrics such as the emergence of novel climates (Williams et al., 2001), changes in area of analogous climate (Ohlemller et al., 2008), changes in a distance to analogous climate (Nogués-Bravo et al., 2010), and climate change velocity (Loarie et al., 2009; VanDerWal et al., 2013), first characterize a climate facet across a given region and then measure local changes in the availability of climate relative to the regional pattern.

Climate change metrics can be used as a proxy for more detailed climate change impact assessments on biodiversity, such as those using species distribution modelling (Garcia et al., 2016). They have also been related to past extinctions (Nogués-Bravo et al., 2010) and species restricted range sizes (Ohlemller et al., 2008; Sandel et al., 2011), demonstrating the usefulness of manipulating climate change data to explore relationships and infer biological phenomena.

Despite the abundance of climate change metrics and their hypothesized links to biodiversity (Garcia et al. 2014), empirical research linking climate change metrics to biodiversity dynamics is still limited. Most often, metric-based explorations of climate change effects on biodiversity use a limited number of variables (e.g., anomalies) despite evidences that suggest single metrics would not capture the wilder range of effects captured by multiple metrics (e.g., Garcia et al., 2014).

One reason for limited exploration of climate change manifestations in climate-change-induced biodiversity impact assessments is that no convenient platform exists where all commonly used metrics are implemented on equal footing. Moreover, the existing tools to quantify the metrics are scattered, substantially different in the way they handle spatiotemporal data, their input and output, and the degree of being user friendly. For example, the velocity of climate change is offered by the “VoCC” R package (García Molinos et al., 2019), while the “analogues” (Hooker et al. 2011) and “extRemes” (Eric Gilleland, 2021) R packages can measure novel climates and extreme value analysis, respectively, each using a different interface. We used a unified interface in the climetrics R package to quantify six different climate change metrics including: 1) Standardized local anomalies; 2) Changes in probability of local climate extremes; 3) Changes in area of analogous climates; 4) Novel climates; 5) Change in the distance to analogous climates; and 6) Climate change velocity.

We have also provided three supporting functions (apply.month, kgc and temporalTrend) to aggregate the time series of climate data over months (i.e., generate 12 outcomes corresponding to 12 months), to classify Köppen climate zones, and to measure the temporal trend at each pixel for a given climate parameter (slope of changes over time), respectively. We attempted to design the functions in the climetrics R package to be user-friendly as they are flexible to handle multiple data formats (e.g., raster or raster time series) while all generating outputs as raster maps. In addition, the package is linked to the “*rts*” R package (Naimi, 2021) for handling raster time series data. The “*rts*” package uses the new R package “*terra*” (Hijmans, 2021b), for manipulating raster data in a very efficient way (i.e., it is substantially faster than many other R packages as its functionalities have been implemented using the C++ programming language). Therefore, *climetrics* can quantify climate change metrics with high computational performance.

# Description of metrics

## Standardized local anomalies

The standardized anomalies metric, also referred to normalized anomalies, quantifies the magnitude of climate change at a pixel level, using a distance measurement in standard units between a data value and its mean. The metric can be calculated by dividing anomalies (the difference from an average or baseline; $t_2$ - $t_1$) to the standard deviation of the interannual variability of the baseline ($t_1$) (Williams et al., 2007).

The Standardized local anomalies metric measures the similarity and dissimilarity between the baseline and a second-time slice (future or past) using the Standardized Euclidean Distance (SED) (Equation 1). Where $t_1$ and $t_2$ are the first and second periods of the climate data, respectively, and $S_{t1}$ is the standard deviation of the interannual variability for the first period ($t_1$).

The standardized local anomalies equally weight all variables, and emphasizes more on the baseline ($t_1$) trends that are larger relative to the second time slice ($t_2$) interannual variability. A higher SED score (Standardized Euclidean Distance; Equation 1) corresponds to a larger local climate changes that is based on the integration of changes in all climate variables involved in the calculation (e.g., minimum and maximum temperature, precipitation).

$$SED = \sqrt{\sum_{k=1}^{n} \frac{(t_{2-}\ t_{1})^{2}}{s_{t1}}}$$

## Changes in probability of local climate extremes

The extreme value theory provides the statistical framework to make inferences about the probability of very rare or extreme events.

Based on the theory of extreme values that derives the Generalized Extreme Value (GEV) distribution, we can fit a sample of extremes to the GEV distribution to obtain the parameters that best explain the probability distribution of the extremes.

The GEV has three parameters: shape, scale, and location (Gaines & Denny, 1993; Katz et al., 2005). The shape of the GEV distribution assumes three possible types: i) a light-tailed (Gumbel), heavy-tailed (Frerchet), and iii) bounded (Weubull) (see Katz et al., 2005). The location parameter specifies where the distribution is “centred”, and the scale parameter is its “spread”.

The *climetrics* R package applies the statistics of extremes presented by Katz et al., (2005). In this method the algorithm calculates the 95th and 5th percentiles of the distributions of the temperature and precipitation, respectively, for each grid cell in the baseline ($t_1$). Then, the percentiles of the future distributions in the second time slice ($t_2$), corresponds to the extreme baseline values, will be calculated. These percentiles correspond to the probability that the historical extremes will be exceeded.

In order to obtain a measure of the probability of extreme events for both temperature and precipitation, and for each grid cell, the algorithm sums the two probabilities and subtracts the product of the two probabilities to avoid counting probabilities twice. The probability of the second time period ($t_2$) is then subtracted from the probability of the first time period ($t_1$). Positive values indicated increased probability of extremes in the second time and negative values indicated a decrease. These calculations capture one single aspect of extreme climates (hot and dry), but other aspects could be calculated in a similar manner.

### Changes in area of analogous climates

The algorithm measures different aspects of a risk arising from climate change by quantifying changes in the spatial distribution of future climate conditions compared with the recent past. To do so, first, the algorithm identifies and maps the updated version of Köppen-Geiger climate classification (Peel et al., 2007) for the baseline ($t_1$) and the second time slice ($t_2$) using temperature and precipitation. The Köppen-Geiger climate classification is based on annual temperature and precipitation after being subjected to a sufficiently large time or ensemble average.

The *climetrics* R package applies the method developed by Ohlemüller et al., (2006) and quantifies climate similarity between areas in both time slices. The algorithm, calculates the changes in areas occupied by a given class between the baseline ($t_1$) and the second time slice ($t_2$) using the ratio (in percentage) of the difference between every grid cell $j$ at $t_2$ (second time slice) and the baseline ($t_1$).

Positive values in a cell indicate gain in area, negative values indicate losses and zero values reflect no changes.

$$\Delta C_{ij} = \sqrt{(C_{t2j} - C_{t1i})^2}$$

$C_{t1i}$ = Raster of Climate classification in $t_1$
$C_{t2j}$ = Raster of Climate classification in $t_2$
$\Delta C_{ij}$ = Area of Analogues climate

## Novel climates

Novel climates are defined as climate environments with no-analogue conditions in the recorded past (Saxon et al., 2005; Ackerly et al., 2010).

The *climetrics* R package uses the method proposed by Williams et al., (2007) to quantify dissimilarities between the baseline ($t_1$) and future/past time slice ($t_2$) using the standardized Euclidean distance (SED; see the Standardized Local Anomalies section).

The algorithm measures the SED for each grid cell between the first ($t_1$) and second time slices ($t_2$). Novel climate is identified by comparing the climate realization of the second time slice ($t_2$) for each grid cell with climate realization of the baseline ($t_1$) for all grid cells, and retaining the minimum SED ($SED_{min}$).

$SED_{min}$ will be equal to or less than the indices of local climate change. The pool of potential climatic analogues is global, so that a high $SED_{min}$ indicates that the second time ($t_2$) has no good analogue anywhere in the baseline ($t_1$).

The larger the score, the more dissimilar the future climate is regarding the global pool of potential climate analogues.

### Change in distance to analogous climates

The *climetrics* R package uses the method developed by Ohlemüller et al., (2006) to quantify climatic similarities between areas.

For a grid cell *i* in the baseline ($t_1$), the algorithm calculates the geographic distance to all other cells *j* that belong to the same climate classification as the grid cell *i*, using great-circle distance following (Zar, 1989). The great-circle distance or orthodromic distance is the shortest distance between two points on the surface of a sphere, measured along the surface of the sphere.

Then for each cell *i*, the algorithm computes the median of the great-circle distance below the 10th percentile of the distribution of all values, for both baseline ($t_1$) and the second time slice ($t_2$), and then maps changes over time. To illustrate the changes in distance between baseline ($t_1$) and second period ($t_2$) at the given climate change level, the algorithm calculates the difference in distance between these times ($\Delta km = km_{t2} - km_{t1}$). A negative value indicates a temporal decrease in the distance, whereas a positive value indicates an increase.

# Climate change velocity

Climate-change velocity is a measure of the local rate of displacement of climatic conditions over Earth's surface (Loarie et al., 2009; Sandel et al., 2011). The *climetrics* R package uses three different algorithms to measure climate change velocity. The first velocity algorithm ("d*Ve*") is a distanced-based velocity, developed by Sandel et al., (2011). Conceptually, this method for calculating velocity is equal to the temporal gradients divided by spatial gradients, and is expressed in units of distance per time (km/year). The algorithm, first, calculates temporal gradient by measuring the local difference between baseline ($t_1$) and second period ($t_2$). Then, it calculates spatial gradients as the slope of the given climate parameter for the baseline ($t_1$) using a 3*3 grid cell neighbourhood.

$$\boldsymbol{dVe\ (km\ /year^{-1}) = \frac{Temporal}{Spatial} = \frac{(t1 - t2\ )year^{-1}}{(Slope\ 3 * 3)km^{-1}}}$$

$t_1$= raster of baseline
$t_2$ = raster of second time period future/past

The second velocity algorithm ("*ve")* in *climetrics*, is implemented based on the method and code developed by Hamman et al., (2015). Since no two grid cells have the same climate value, the algorithm uses a user-defined threshold to find a climate match for the baseline climate surface in a climate surface representing a second period ($t_2$). Then, it calculates the geographic distance of all matching $t_2$ climate cells to the baseline cell and finds the shortest geographic distance. This distance is divided by the number of years between the $t_1$ and $t_2$ climate providing the metric of velocity (see Hamann et al., 2015).

The third algorithm of climate change velocity (“gVe”) is a gradient-based method that follows the method presented by (Burrows et al., 2011). In this approach, the velocity is calculated by dividing long term trend of climate parameters by the spatial gradient along that direction. For an angle, θ, with 0° as North and 180° as South, the velocity of climate change along that angle, Vθ, is given by:

$$\boldsymbol{V\theta = \frac{Temporal\ trend}{S_{NS}\ cos\theta\ \ + S_{EW}\ \ sin\theta}}$$

where $S_{NS}$ is the North-South spatial gradient and $S_{EW}$ is the East-West spatial gradient. When θ is perpendicular to the angle of the velocity of climate change, the velocity of climate change in that direction is infinite, since the denominator in equation 8 becomes zero.

## Package overview and features

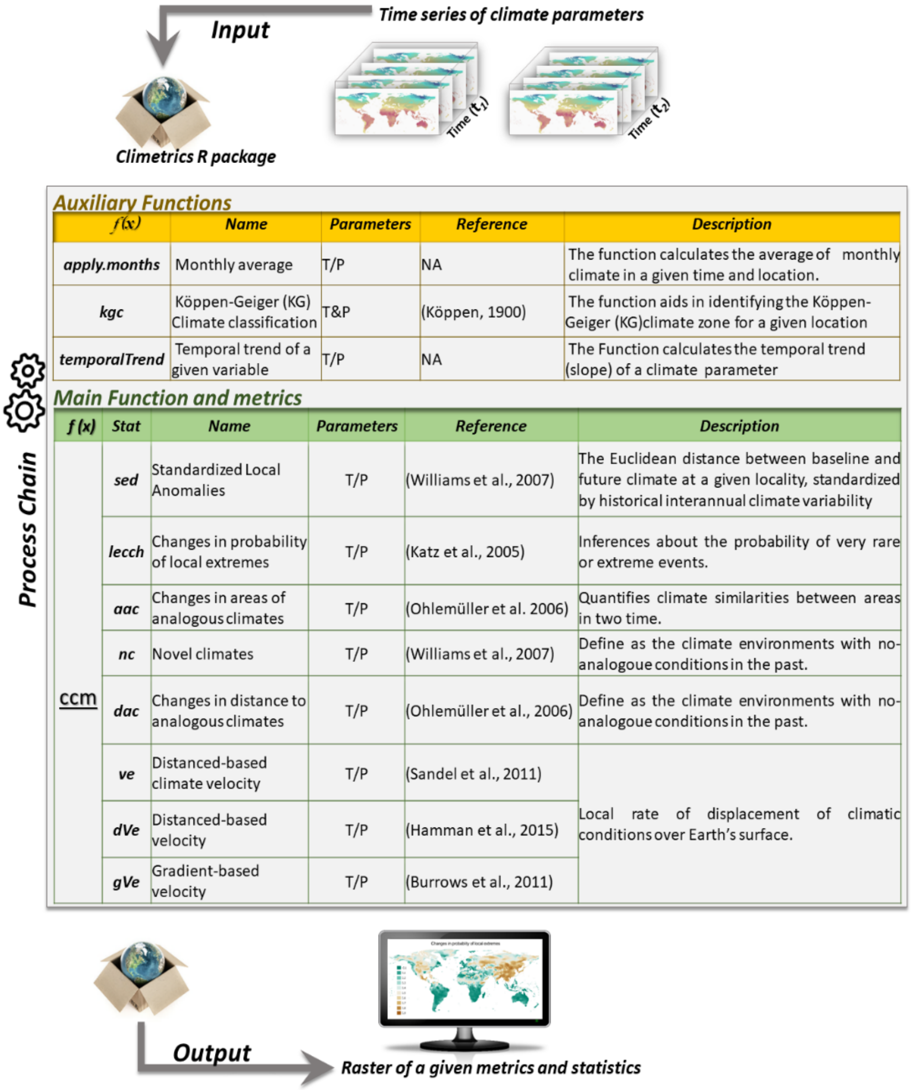
The *climatrics* R package contains a separate function to quantify each climate change metric, also a function (“*ccm”*) to quantify some or all the six metrics together. In addition, some other functions are provided by the package including “*apply.months”*, “*kgc”,* and “*temporalTrend*” (Figure 1). The “*apply.months”* is an auxiliary function that calculates monthly statistics from time series of climate data. The output of *apply.months* contains twelve raster layers (from January to December). For instance, a user can choose the mean function as the input to calculate the monthly mean climate data for the 12 months. The kgc is another auxiliary function to calculate Köppen-Geiger (see Köppen, 1900; Peel et al., 2007) classification of climate data in a given location and time. The Köppen-Geiger system classifies the climate zones of the world into five main classes and 30 sub-classes (D. Chen & Chen, 2013; Beck et al., 2018) and is based on threshold values (See table S1 for criteria and legend) and seasonality of monthly temperature and precipitation. The KG is the main element for calculating the Changes in Distance to Analogous Climates (dac) metrics in the “*climetrics”* function. The “*temporalTrend”* functions quantifies the trend and pattern of climate parameters over time. A higher positive slope of the given climate parameter means increas over time and negative values shows temporal decline over time.

The *climetrics* is an open-source package hosted on GitHub (https://github.com/Shirin-t/climetrics) and CRAN that is freely accessible for all R users.

The *climetrics* package works with raster time series data and depends on series of R packages: “*rts”* (Naimi, 2021), “*raster*”(Robert J. Hijmans, 2021a), and “*terra*” (Robert J. Hijmans, 2021b) to be installed and loaded.

To illustrate the use of *climetrics* package, we created a few examples of input, process and outputs of the package that can be easily reproduced and used by users.

As an example, we used a time series of global climate data from the updated version of the Climate Research Unit’s database (http://www.cru.uea.ac.uk). The temporal resolution of the data is 120 years from 1901 to 2020, and the spatial resolution 0.5 degrees. We sliced climate data for a 30-year interval. The baseline ($t_1$) covered 30 years from 1901 to 1930, and the second period ($t_2$) from 1991 to 2020. Figure 2 provides a simple example on interfacing *climetrics* through command line and some outputs. Further examples are provided in the tutorial.



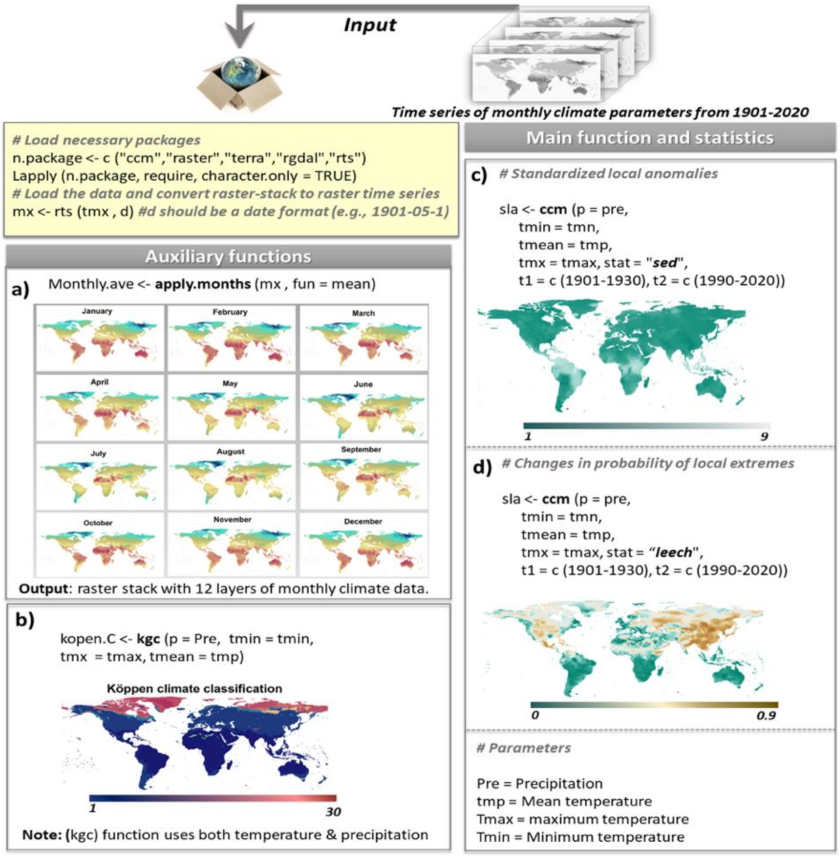
**Auxiliary Functions**

| f(x) | Name | Parameters | Reference | Description |
|---|---|---|---|---|
| ***apply.months*** | Monthly average | T/P | NA | The function calculates the average of monthly climate in a given time and location. |
| ***kgc*** | Köppen-Geiger (KG) Climate classification | T&P | (Köppen, 1900) | The function aids in identifying the Köppen-Geiger (KG)climate zone for a given location |
| ***temporalTrend*** | Temporal trend of a given variable | T/P | NA | The Function calculates the temporal trend (slope) of a climate parameter |

**Main Function and metrics**

| f (x) | Stat | Name | Parameters | Reference | Description |
|---|---|---|---|---|---|
| ccm | ***sed*** | Standardized Local Anomalies | T/P | (Williams et al., 2007) | The Euclidean distance between baseline and future climate at a given locality, standardized by historical interannual climate variability |
| | ***lecch*** | Changes in probability of local extremes | T/P | (Katz et al., 2005) | Inferences about the probability of very rare or extreme events. |
| | ***aac*** | Changes in areas of analogous climates | T/P | (Ohlemüller et al. 2006) | Quantifies climate similarities between areas in two time. |
| | ***nc*** | Novel climates | T/P | (Williams et al., 2007) | Define as the climate environments with no-analogoue conditions in the past. |
| | ***dac*** | Changes in distance to analogous climates | T/P | (Ohlemüller et al., 2006) | Define as the climate environments with no-analogoue conditions in the past. |
| | ***ve*** | Distanced-based climate velocity | T/P | (Sandel et al., 2011) | Local rate of displacement of climatic conditions over Earth's surface. |
| | ***dVe*** | Distanced-based velocity | T/P | (Hamman et al., 2015) | |
| | ***gVe*** | Gradient-based velocity | T/P | (Burrows et al., 2011) | |

**Fig III.1.A** schematic representation of the "climetrics" R package. The six climate change metrics (green table) and three auxiliary function (yellow table) are available in "climetrics" R package. The name, reference and short description of each function and statistics are shown. The number of parameters for each metrics depends on the aim of the user, however, for some functions like (kgc) both precipitation (P) and temperature (T) should be provided.



```
# Load necessary packages
n.package <- c ("ccm","raster","terra","rgdal","rts")
Lapply (n.package, require, character.only = TRUE)
# Load the data and convert raster-stack to raster time series
mx <- rts (tmx , d) #d should be a date format (e.g., 1901-05-1)
```

a)

```
Monthly.ave <- apply.months (mx , fun = mean)
```

**Output**: raster stack with 12 layers of monthly climate data.

b)

```
kopen.C <- kgc (p = Pre,  tmin = tmin,
tmx  = tmax, tmean = tmp)
```

**Note:** (kgc) function uses both temperature & precipitation

c)

```
# Standardized local anomalies
sla <- ccm (p = pre,
    tmin = tmn,
    tmean = tmp,
    tmx = tmax, stat = "sed",
    t1 = c (1901-1930), t2 = c (1990-2020))
```

d)

```
# Changes in probability of local extremes
sla <- ccm (p = pre,
    tmin = tmn,
    tmean = tmp,
    tmx = tmax, stat = “leech",
    t1 = c (1901-1930), t2 = c (1990-2020))
```

*# Parameters*

Pre = Precipitation
tmp = Mean temperature
Tmax = maximum temperature
Tmin = Minimum temperature

**Fig III.2**.An example of using ‘climetrics’ package in R that demonstrates loading data and necessary packages, read data and use some of the functions. The yellow panel shows loading necessary packages and converting data to time series format. a) illustrates the codes and output of the “apply.month” auxiliary function. The function uses a raster stack or raster time-series to generate the statistics monthly average, standard deviation, median on the statistics used (e.g., mean, standard deviation) calculates the monthly average of the time series data. b) shows the kgc function, which calculates Köppen climate classification and uses outputs of “apply.month”. Pannes c&d show examples of functions used to calculate two metrics of climate change; c) Standardized local anomalies and d) changes in probabilities of local extremes. High values in both maps correspond to large changes in temperature and precipitation and high probability of local extremes respectively.

# Conclusion

The univariate climate change attribution and simple anomalies have been widely documented in biodiversity conservation and other sectors. However, climate is intrinsically multivariate and many organisms and socio-ecological systems are adapted to or impacted by multiple variables and their interactions (Dobrowski et al., 2013; Mora et al., 2018; Abatzoglou et al., 2020). This highlights the need for a set of appropriate and standard measurements to capture the complexity of climate change. The development of "*climetrics*" R package provides an easy-to-use comprehensive set of functions for capturing different dimensions of climate change and apply them in modelling and monitoring the biodiversity. The package should provide a set of useful tools to map the complexity in climate change using multivariate climate parameters and more sophisticated methods rather than simple anomalies used in most of studies.

# **IV CHAPTER.** EXPOSURE OF GLOBAL THREATENED SPECIES TO CLIMATE AND LAND-USE CHANGES OVER THE CENTURY

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Shirin Taheri1 & Miguel B. Araújo

Manuscript in preparation

# Exposure of global threatened species distributions to climate and land-use changes over the past century

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Manuscript in preparation

# Abstract

According to IUCN, 28.5% of vertebrates and plants are currently threatened with extinction. Underlying causes are varied but changes in climate and land use figure among the suspected culprits. Quantifying exposure of threatened species to environmental drivers is critical for conservation management, but such a process has been hampered by limited consideration of multiple dimensions of change, namely climate. Using a comprehensive characterization of historical climate and land-use changes during the 20th century, we mapped ten risks from five climate change dimensions and five land-use transitions and compared the ensuing patterns with diversity patterns among threatened amphibians, birds, mammals, reptiles, and plants species. We then calculated the proportion of threatened species that were impacted by multiple dimensions of climate and land-use change in isolation and

combination. We show that threatened species in the Caribbean and Latin America, as well as Southeast and South Asia, were exposed to the greatest amount of co-occurring threats. 10% of globally threatened species face an extremely high risk for both climate and land-use change. Understanding the Spatio-temporal patterns of threats could significantly enhance our ability to direct efforts to areas where the greatest conservation outcomes can be delivered.

## Introduction

Conversion of natural habitats to crop, pasture, and infrastructure together with climate change, are among the major threats to biodiversity (WWF, 2020), threatening to drive tens of thousands of species to extinction (IUCN, 2021).

Despite this, we still have limited information about the spatial pattern and intensity of the threats of this crisis (e.g., Allan et al., 2019; Harfoot et al., 2021). This is particularly true for pressures such as multiple risks of climate change (e.g., frequency and magnitude of extreme events or speed and direction of climate change, etc.). Because, each dimension of climate change affects biodiversity in different ways (Garcia et al., 2014); for example, not all species are at equal risk of climate change velocity (Davies et al., 2009). Strong disperses should be most able to maintain distributional equilibrium with climate conditions and are therefore likely to occupy more of their potential range and avoid extinction (Sandel et al., 2011). Extreme climate events and standardized anomalies are expected to alter the distribution of the population of individual species or community responses such as changes in species richness, composition or dominance (R. M. B. Harris et al., 2020) and Novel climates have been suggested to be associated with species assemblages (Williams et al., 2007).

Evidence suggests that there is a strong spatial variation in the intensity of anthropogenic pressures and threats are not evenly distributed across the Earth (e.g., Allan et al. 2019). This implies that some of the threatened species in different regions of the world have been exposed to complex and co-occurring drivers (e.g., Bowler et al., 2020).

Understanding and quantifying spatial patterns of where land-use activities such as deforestation, agricultural intensification, grass-land expansion and human settlement overlap with local and regional climate change metrics, will improve our ability to prioritise actions to manage and mitigate threats to biodiversity.

To our knowledge, no efforts undertaken at either regional or global extents have accounted for the spatial heterogeneity and alternative dimensions of climate and land-use change on the distribution of threatened species.

Past efforts that provided spatial patterns of threats focused on some human impacts (Allan et al., 2019; Harfoot et al., 2021) and simple climate change anomalies (e.g., Howard, Flather, and Stephens 2020) and failed to account for the multidimensional nature of climate and land-use change.

Here, we mapped the global distribution of risks associated with the five climate change metrics (temporal slope of temperature & precipitation; standardized local anomalies; velocity of climate change & extreme events) and historical land dynamics (forest loss, crop gain, land frequency change and pasture gain) as well as urban spread as threats to the globally threatened species of reptiles, plants, mammals, birds and amphibians over the past century (1900-2020). We then provided a global estimation of high-risk areas for threatened species due to the concurrent impact of climate and land-use change over the 20th century and calculated the proportion of threatened species in areas with extremely high to low risk of climate and land-use change in isolation and combination.

# Methods and materials

## Species occurrence records

Species range maps of threatened species of mammals, amphibians, reptiles and plants were derived from (IUCN, 2021), whilst distributions data from bird species were obtained from BirdLife International (BirdLife, 2017). The list of threatened species were those classified as either “vulnerable”, “endangered” or “critically endangered” by the IUCN. Using these categories, we selected (n = 19333) occurrences of threatened species for our analysis.

Data were available as spatial polygons of distribution boundaries, which were projected onto the Latitude/Longitude projection-WGS 84 and converted to a grid with a cells size of 0.5 degrees (the same cell size as climate data). Where a species’ range polygon intersected with a grid cell, the species was treated as present within the entire cell. The total species richness was calculated as the total number of species present in a grid cell. Total species richness and total threatened species richness were also calculated for the five individual taxonomic groups (mammals, amphibians, reptiles, plants and birds). Since the distribution of threatened species strictly follows the simple formula that “the higher species richness, the higher the number of threatened taxa”, we reduced this effect by using the residuals of threatened species richness when explained by total species richness.

## Climate data

We obtained the global time series (1901-2020) of maximum and minimum temperature and annual precipitation at a spatial resolution of 0.5 degrees from the updated version of the Climate Research Unit’s database (I. Harris et al., 2020). The baseline covered the period (from 1901-to 1930) and the second time (from 1990-to 2020).

Conceptually, the existing metrics of climate change can be aggregated into local or regional (Garcia et al., 2014). Local climate change metrics such as anomalies (M. B. Araújo et al., 2008), standardized local anomalies (Williams & Jackson, 2007), probability of extreme events (Jiménez et al., 2011) and seasonality (Lane et al., 2012), characterize the magnitude of changes by quantifying how average or extreme values in the frequency distribution of climate change data series are altered in a given locality (cell or pixel in a raster layer) over time. In turn, regional metrics such as climate change velocity (Loarie et al., 2009; VanDerWal et al., 2013), novel climates (Williams et al., 2001), changes in the area of analogous climate (Ohlemller et al., 2008) and changes in distance to analogous climate (Nogués-Bravo et al., 2010), first characterize a climate facet across a given region and then measure local changes in the availability of climate relative to the regional pattern.

In order to quantify and map the complexity of climate change, we chose three local (temporal trend temperature & precipitation, standardized local anomalies & probability of extreme events) and one regional (velocity) climate change metric. The five metrics were chosen because they showed the most notable changes in climate parameters during the last century. To determine the intensity of climate change, we combined these four metrics as a single raster layer. The higher the values of pixels in the output raster, the more complex climate change was experienced in these cells (areas) during the last century.

However, since the raster outputs of each metric have different scales and values, we rescaled all the outputs of metrics, ranging from 0 to 1, before combining them. Because, when an analysis calls for multiple rasters to be combined mathematically, it is often recommended to have the values in each raster converted to a standard scale. Then we classified the intensity of climate change as extremely high if the value of a pixel in the output raster was ($x > 0.75$), high if the value of pixel was ($0.55< x <0.75$), moderate risk if the values lie ($0.30< x <0.55$) and low risk if the value was ($x <0.30$). We then calculated the proportion of threatened species in extremely high to low risk of climate change.

Calculations of metrics were performed using "*Climetrics*" R package version 1.3 (Chapter III) and the rest of the analysis in R version 1.2.5019.

### Land-use change

We used the global dataset of historic land dynamic assessments between (1960-2019) at 1km spatial resolution (Winkler et al., 2021). HILDA (Historic Land Dynamics Assessment) is based on a data-driven reconstruction approach and integrates multiple open data streams from high-resolution remote sensing, long term land-use reconstructions and statistical analysis. HILDA data set presents the gains and losses in major land use categories during the last sixty years. Here we used the change dynamics of forest, croplands and pasture/rangeland as well as land change frequency (number of times that a pixel has changed).

The global human settlement layer (GHSL) was obtained from the official website of the European Union (https://ghsl.jrc.ec.europa.eu) at 1km spatial resolution. The GHSL is open access and free data, offering global spatial information, evidence-based analytics, and knowledge describing the human presence on the planet in the past: 1975, 1990, 2000 and 2014 extracted from Landsat images (Marcello et al., 2019). Human settlements and build-up areas are characterized by constructed, man-made objects including buildings and associated structures and civil works.

The proportion of individual land-use categories was calculated within each 0.5 degree as climate dataset. We then classified the percentage of each land-use category as extremely high if the value of a pixel shows high land change ($x > 0.75$); high risk if the value of a pixel is ($0.55< x <0.75$); medium risk if the value of a pixel is ($0.30< x <0.55$) and low risk if the value is ($x < 0.30$). We then calculated the proportion of threatened species in high to low-risk areas of land-use change.

### Data analysis

To explore the association between individual variables and global patterns in threatened species richness, we fitted a polynomial linear model and used an analysis of variance (ANOVA). This was performed for all threatened species richness (when explained by total species richness) in thirty subclasses of the Köppen-Geiger climate classification. The Köppen climate classification divides the earth's climate into five main classes and thirty subclasses based on precipitation and heat (Köppen, 1900; Peel et al., 2007). We then partitioned the variation of each variable in each subclass of Köppen-Geiger climate classification. To calculate the proportion of variance explained, we divided the sum of squares between groups by the total sum of squares. A higher percentage of explained variance indicates the strength of association.

We then used Random Forest to assess the potential impacts of the climate and land-use change on the distribution of threatened species. A random forest is a machine learning technique that is made from multiple decision trees, each tree individually predicts the new data and the output of the random forest is the class selected by most trees. Random forests are recognized to be robust and produce good predictive models (Breiman, 2001).

Here, we used 2000 trees and 50 replications of Random Forest to find the importance of each climate and land-use variable using the Mean Decrease Accuracy table. This importance is a measure of how much removing a variable decreases the accuracy. We perform Random Forest in each main class of Köppen-Geiger climate classification (tropic, temperate, arid, continental and polar). We applied Variance Inflation Factor (VIF) and absolute correlation coefficient to test multicollinearity between predictor variables in each main class of Köppen-Geiger climate zones. Multicollinearity test between variables showed that in Tropic, the temporal trend in temperature (Trendtem) was highly correlated with Extreme climate events (VIF value > 10 & absolute correlation coefficient of > 0.9) and was removed from the model. We found another collinearity between variables in the Temperate climate zone, in which temporal trend in temperature, standardized local anomalies and Extreme climate events were highly correlated (VIF value > 10 & absolute correlation coefficient > 0.7). Therefore, we removed temporal changes in temperature and standardized anomalies and applied the model with the rest of the variables. Models were fitted using the “randomForest” package in R (Liaw & Wiener, 2002).

In both methods we first, modelled threatened species richness in relation to the total species richness alone. Second, we used the residuals of this model to fit the random forest and find the importance of each climate and land-use variable. All analyses were carried out in R 3.3.1 (R Core Team 2019).

## Results

The combination of five climate change metrics revealed the spatially heterogeneous risks of climate change over the past century.

Countries in Southern and Eastern Asia, the Caribbean, a large part of the United States, Central Europe, and both Eastern and Southern Africa have been among the most exposed to high rates and complex climate change patterns in the last hundred years (Fig IV.1a). These regions have experienced, the multiple dimensions of climate change. Southeast Asia (e.g., Indonesia, Malaysia, Philippines) for example, apart from high local standardized anomalies, have been exposed to high extreme events and high temporal changes in temperature and precipitation. In addition to the climate, land-use change such as forest loss, and crop/pasture gains also showed a spatially divergent pattern (Fig IV.1-b) which in some areas coincides with a high rate of climate change (Fig IV.1-c).

The map shows large parts of India, China, Southern Russia, The Caribbean, Brazil, and a large part of Australia is among regions with a high level of both climate and land-use change.

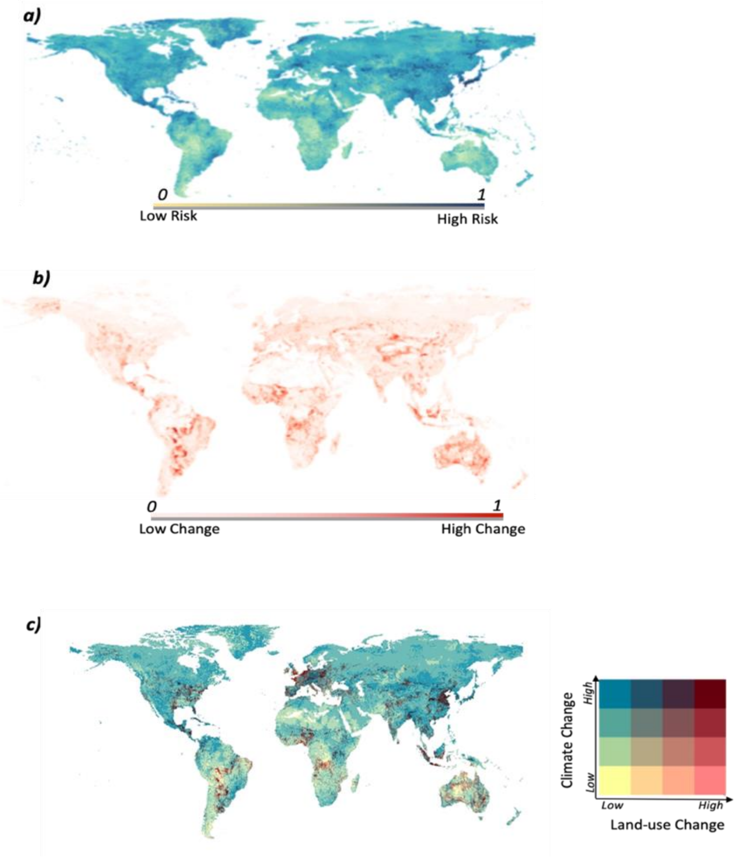


**Fig IV.1.** Geographic distribution of risks from multiple dimensions of climate and land-use change over the past century. (a) The combination of five climate change metrics (temporal slope of temperature & precipitation; standardized local anomalies; velocity of climate change & extreme events (from 1901 to 2020). A value of 0 indicates no or low risk in climate, and 1 indicates areas with an extremely high risk of climate change. (b) The combination of land-use changes (forest loss, crop gain & pasture gain from 1960-2020 and human settlement (1975-2014). A value of 0 indicates no or low level of land change, and 1 indicates areas with an extremely high risk of land change. (c) Bivariate choropleth map overlapped climate change and land-use change. The dark red colour indicates areas that experienced an extremely high level of both climate and land change during the last century and can be considered as extremely high risk for biodiversity. The risk classification of joint climate and land-use change is as follows: extremely high risk (x > 75%); high risk if the value of a pixel is (0.55< x <0.75); medium risk if the value of a pixel is (0.30< x <0.55) and low risk if the value is (x < 30%).

Assessing the risk of climate change alone shows that over the past century, threatened species in the Caribbean, the Amazon, Southeast Asia and East Africa have been exposed to multiple dimensions of climate change (Fig IV.2 a, b, c, d, e).

Threatened species in Southeast Asia (e.g., Malaysia, Indonesia), Caribbean counties, a large part of Brazil, southern India and Eastern Africa (e.g., Kenya, Uganda, Tanzania and Rwanda) have been exposed to the high probability of extreme events, standardized local anomalies and high rate of warming (trend change) over the past century. While, threatened species in North America, a large part of Russia, Eastern Europe, central Australia and Southern & Northern Africa have been exposed to the high level of climate change velocity (speed and direction of climate change).

We found that over the past century (7 - 23.2) % of threatened reptiles; (5.3 - 24) % of plants; (5.2 - 26.1) % of mammals; (5.1 - 24.7) % of birds and (11 - 30) % of amphibians have been exposed to extremely high or high risk of multiple dimensions of climate change respectively (Fig IV.2 f).

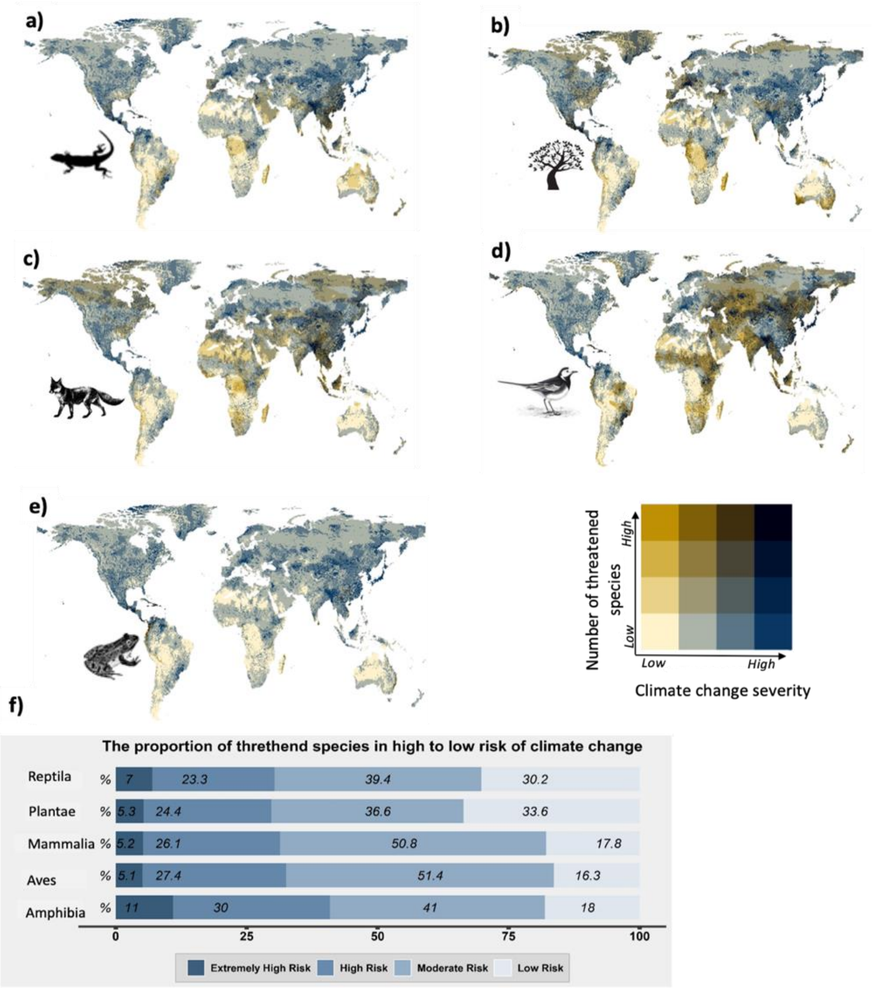


**Fig IV.2.** The exposure of threatened species richness to multiple dimensions of climate change over the past century (1901-2020). Bivariate choropleth maps combine risk of climate change and threatened species richness when explained by total species richness for (a) reptiles, (b) plants, (c) mammals, (d) birds and (e) amphibians. Dark areas show the extremely or high risk of climate change with high number of threatened species. (f) The proportion of threatened species in extremely high to low risk of climate change. The risk classification of climate change is as follows: extremely high risk if the value of a pixel is (x > 75%); high risk if the value of a pixel is (0.55< x <0.75); medium risk if the value of a pixel is (0.30< x <0.55) and low risk if the value is (<30).

Exploring the risk of land-use on threatened species richness shows that land change has a complex and divergent pattern. For example, threatened species in Southern and Central Russia, Madagascar, Brazil, the Caribbean, Paraguay, Bolivia, Northern Argentina, Southeastern Asia and central Africa were impacted by high deforestation rates. While, species in India, Eastern China, the USA and Europe were impacted by agriculture intensification (crop gain). Grazing expansion is affecting species in Australia, Brazil, a large part of China and western and southern Africa.

Overall threatened species in southeast Asia (e.g., Myanmar, Indonesia, Cambodia), a great part of China, Australia, the Caribbean, western and central Africa, Brazil, Amazonia and southern Russia have been affected by multiple drivers associated with land-use changes (e.g., deforestation, agricultural intensification, urbanization or grassland expansion) (Fig IV -3 a, b, c, d, e). We found that in the last six decades, (4.7 - 7.4) % of reptiles, (6 - 8.3) % of plants, (3 - 4.7) % of mammals, (3.3 - 5.2) % of birds and (4.4 - 9) % of amphibians have been exposed to an extremely high or high level of land-use intensification respectively (Fig IV-3 f).

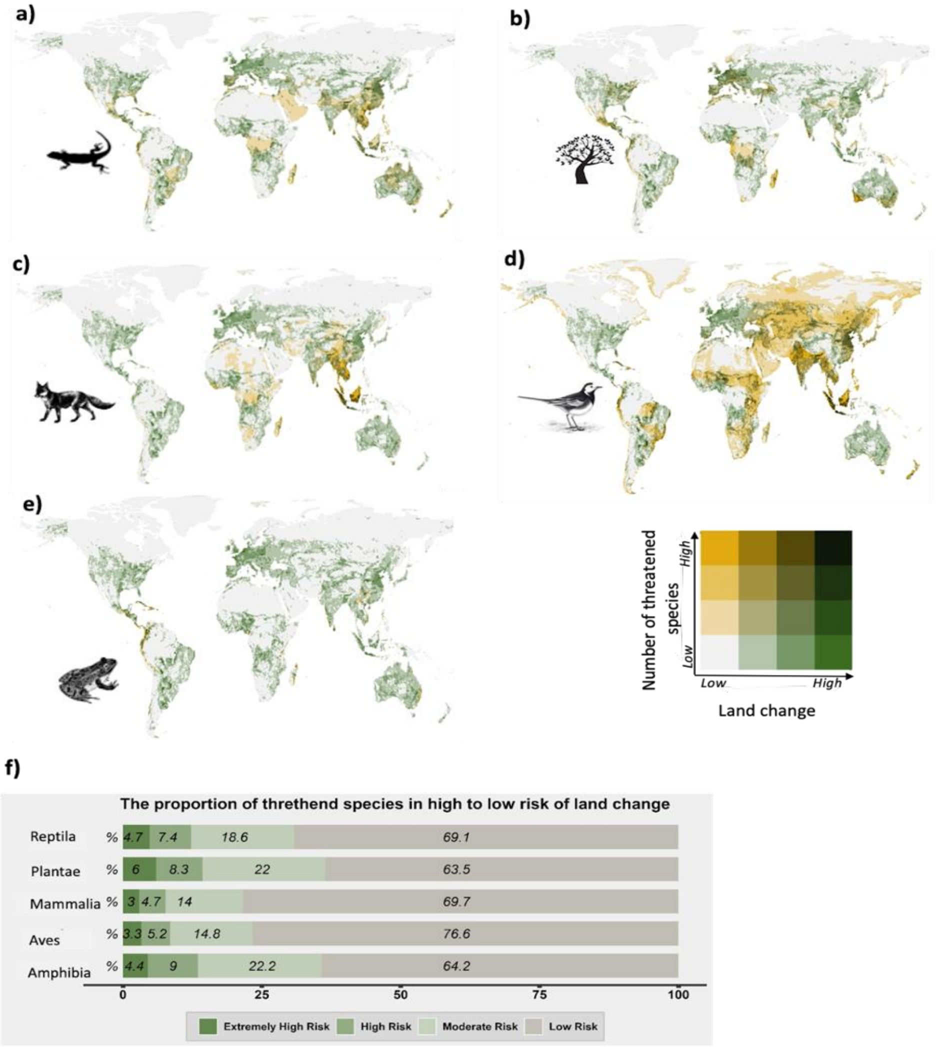


**Fig IV.3.** The exposure of threatened species richness to the historical land-use change (1960-2020). Bivariate choropleth maps combine risk of land-use change and threatened species richness when explained by total species richness for (a) reptiles, (b) plants, (c) mammals, (d) birds and (e) amphibians. Dark areas show the extremely high risk of land-use change with high number of threatened species. (f) The proportion of threatened species in extremely high to low risk of land-use changes over the past sixty years. The risk classification of land-use are as follows: extremely high if the value of a pixel is (x>75%); high risk if the value of a pixel is (0.55< x <0.75); medium risk if the value of a pixel is (0.30< x <0.55) and low risk if the value is (x<30%).

The combined forces of climate and land-use change showed that over the past century, threatened species in South-eastern Asia (e.g., Indonesia, Malesia, Thailand), eastern and central Africa, Madagascar, the Caribbean and southern India are exposed to a high risk of both climate and land-use change (Fig IV-4 a). Our results revealed that (3 - 14.3) % of threatened reptiles, (2 - 8.8) % of plants; (1.3 - 6.1) % of mammals; (1.3 - 6.3) % of birds and (2.6 - 10.5) % of amphibians have been exposed to extremely high to high risk of both climate and land-use change respectively (Fig IV-4 b). It means threatened species in these regions, in addition to the major land-use change (>75% of changes in the land), faced a high rate of climate change.

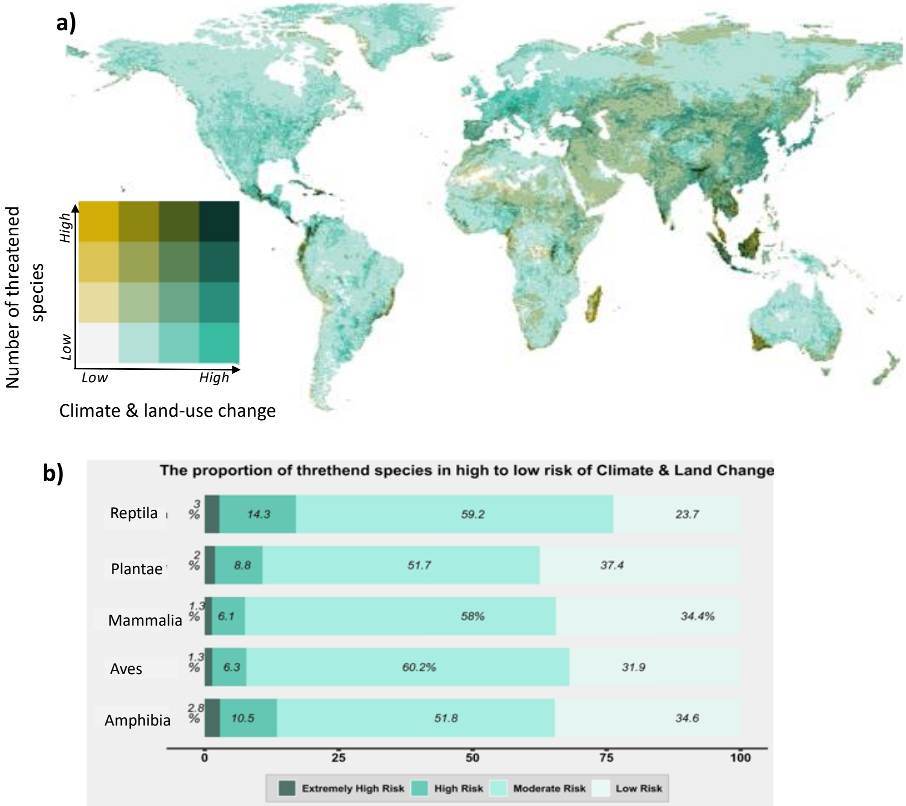


**Fig IV.4**.Global footprint of climate and land change on threatened species distribution over the past century. (a) The bivariate choropleth map shows the areas with extremely high to low levels of risks from climate and land change overlapped with threatened species richness when explained by total species richness. Dark areas indicate a high level of risks from both climate and land change and a high number of threatened species. (b) The barplot shows the proportion of species that experienced extremely high to low risk of climate change and land change. The risk classification of joint climate and land change is as follows: extremely high if the value of a pixel is (x>75%); high risk if the value of a pixel is (0.55< x <0.75); medium risk if the value of a pixel is (0.30< x <0.55) and low risk if the value is (x<30%).

The global assessment of climate and land-use change revealed that threatened species are affected by multiple co-occurring threats (Fig IV-5 a, b, c, d, e).

Threatened species in the Tropics, for example, have been exposed to high risk of both climate (e.g., extreme climate events & temporal trends in temperature) and land-use change (e.g., agricultural expansion and land frequency change) (Fig IV-5 a). In the Continental climate zone, after crop-rising, extreme climate events and trends in precipitation change were in second and third place respectively (Fig IV-5 b).

Threatened species richness in temperate zones have been exposed to high extreme climate events, velocity, land frequency change and deforestation rate (Fig IV-5 c). The arid climate zone has been affected by the high risk of standardized local anomalies, trends in precipitation, land frequency change and forest loss (Fig IV-5 d), and threatened species in the Polar zone, have been affected by the high rate of temporal trend in both temperature and precipitation over the last century (Fig IV-5 e).

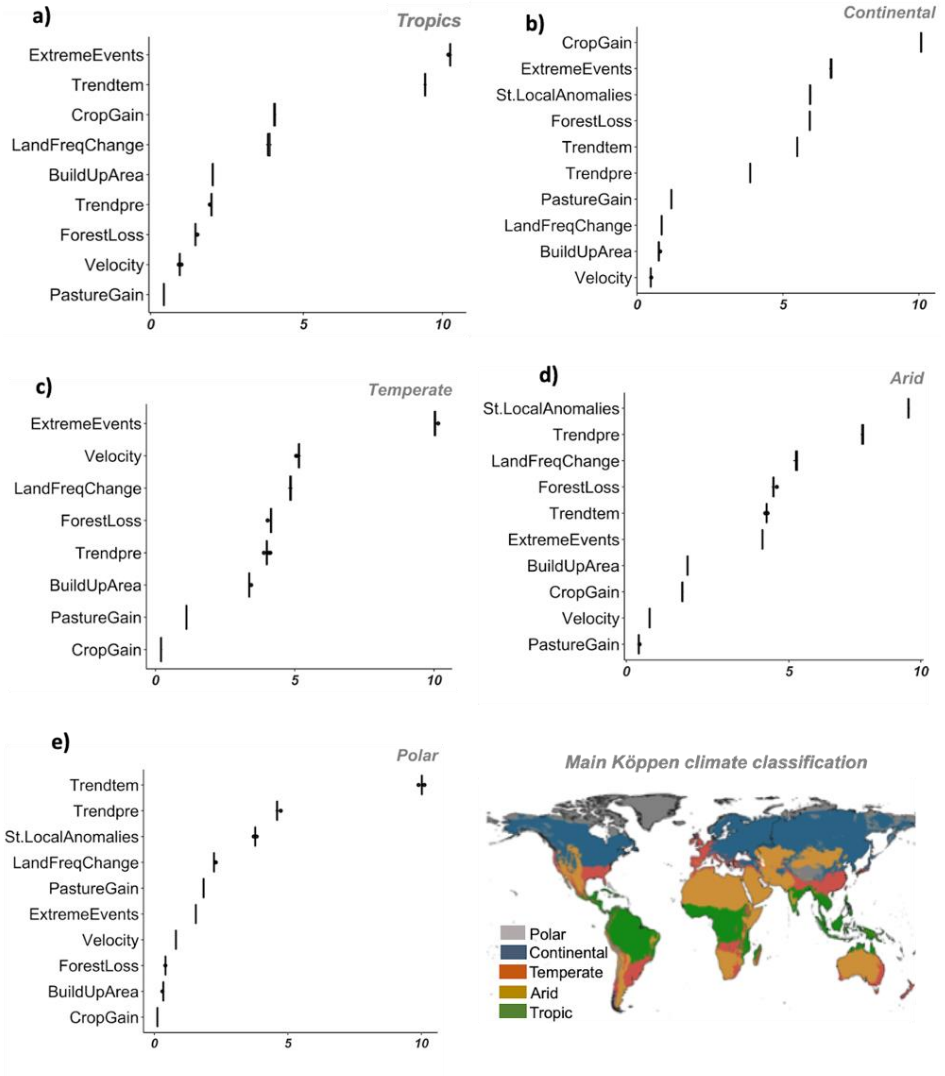
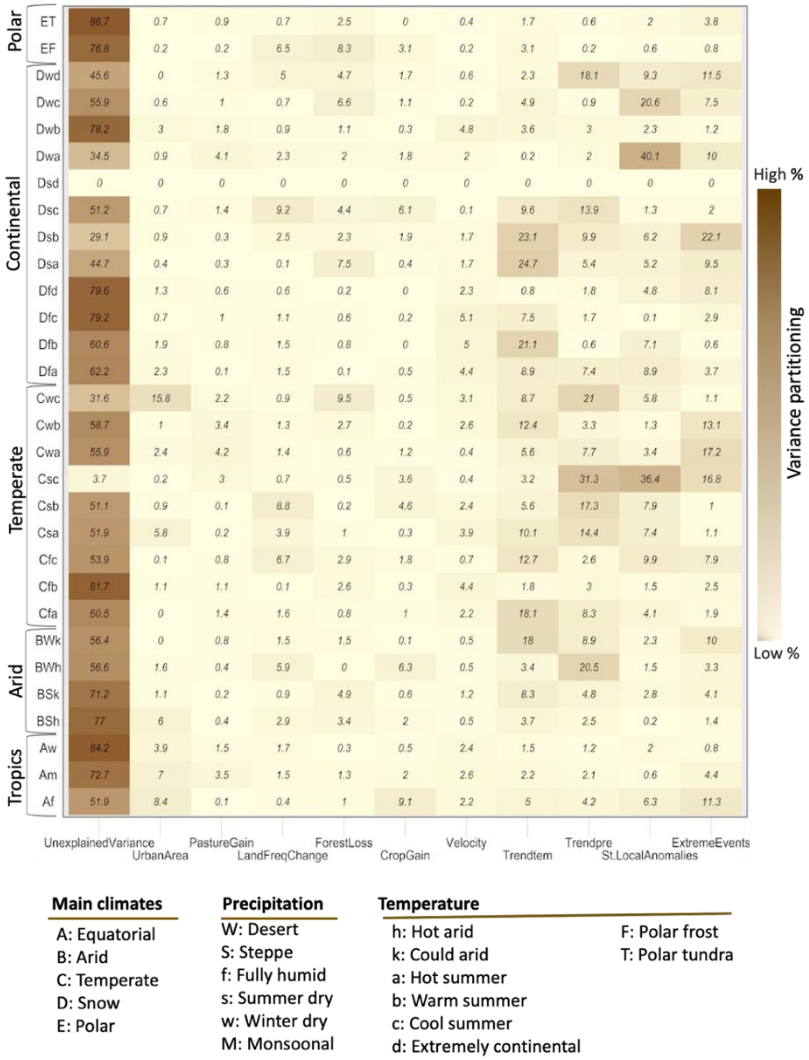


**Fig IV.5**.Variable importance obtained from Random Forest in each main Köppen-Geiger climate classification. The panels illustrate the importance of multiple dimensions of climate and land-use change on threatened species richness when explained by total species richness in (a) Tropics, (b) Continental, (c) Temperate, (d) Arid and (e) polar climate zones. The X-axis shows the mean decrease accuracy (mean decrease in Gini coefficient) and measures how variables contribute to the model. The higher the value of mean decrease accuracy or mean decrease Gini score, the higher the importance of the variable in the model.

The association between threatened species richness and multiple threats determined the strong spatial variation in the intensity and magnitude of climate and land-use change. Overall, extreme climate events, standardized local anomalies, temperature and precipitation trends were the top four drivers for globally threatened species richness over the past century (Fig IV-6). When aggregated climate and land-use change in thirty Köppen-Geiger classifications, we found that the high climate change impacts are in almost all subclasses of Temperate and Continental climate zones. The exposure of threatened species richness to land use was also high in both regions. In the CwC subdivision of the Köppen-Geiger climate (Temperate winter-dry & cool-summer), for example, urbanization and forest loss explained (15.8) % and (9.5) % of the distribution of threatened species richness, respectively after the precipitation trend. In the Csc subdivision of the Köppen-Geiger climate (Temperate summer-dry & cool-summer), most of the variations of threatened species were explained by multiple threats from climate change.

Other examples could be the Dwa subdivision of the Köppen-Geiger climate, which is (Continental winter-dry & hot-summer) which is located in eastern China, North and South Korea that showed high exposure of threatened species to standardized local anomalies (Fig 5-6).



| | | UnexplainedVariance | UrbanArea | PastureGain | LandFreqChange | ForestLoss | CropGain | Velocity | Trendtem | Trendpre | St.LocalAnomalies | ExtremeEvents |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Polar | ET | 86.7 | 0.7 | 0.9 | 0.7 | 2.5 | 0 | 0.4 | 1.7 | 0.6 | 2 | 3.8 |
| | EF | 76.8 | 0.2 | 0.2 | 6.5 | 8.3 | 3.1 | 0.2 | 3.1 | 0.2 | 0.6 | 0.8 |
| Continental | Dwd | 45.6 | 0 | 1.3 | 5 | 4.7 | 1.7 | 0.6 | 2.3 | 18.1 | 9.3 | 11.5 |
| | Dwc | 55.9 | 0.6 | 1 | 0.7 | 6.6 | 1.1 | 0.2 | 4.9 | 0.9 | 20.6 | 7.5 |
| | Dwb | 78.2 | 3 | 1.8 | 0.9 | 1.1 | 0.3 | 4.8 | 3.6 | 3 | 2.3 | 1.2 |
| | Dwa | 34.5 | 0.9 | 4.1 | 2.3 | 2 | 1.8 | 2 | 0.2 | 2 | 40.1 | 10 |
| | Dsd | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Dsc | 51.2 | 0.7 | 1.4 | 9.2 | 4.4 | 6.1 | 0.1 | 9.6 | 13.9 | 1.3 | 2 |
| | Dsb | 29.1 | 0.9 | 0.3 | 2.5 | 2.3 | 1.9 | 1.7 | 23.1 | 9.9 | 6.2 | 22.1 |
| | Dsa | 44.7 | 0.4 | 0.3 | 0.1 | 7.5 | 0.4 | 1.7 | 24.7 | 5.4 | 5.2 | 9.5 |
| | Dfd | 79.6 | 1.3 | 0.6 | 0.6 | 0.2 | 0 | 2.3 | 0.8 | 1.8 | 4.8 | 8.1 |
| | Dfc | 79.2 | 0.7 | 1 | 1.1 | 0.6 | 0.2 | 5.1 | 7.5 | 1.7 | 0.1 | 2.9 |
| | Dfb | 60.6 | 1.9 | 0.8 | 1.5 | 0.8 | 0 | 5 | 21.1 | 0.6 | 7.1 | 0.6 |
| | Dfa | 62.2 | 2.3 | 0.1 | 1.5 | 0.1 | 0.5 | 4.4 | 8.9 | 7.4 | 8.9 | 3.7 |
| Temperate | Cwc | 31.6 | 15.8 | 2.2 | 0.9 | 9.5 | 0.5 | 3.1 | 8.7 | 21 | 5.8 | 1.1 |
| | Cwb | 58.7 | 1 | 3.4 | 1.3 | 2.7 | 0.2 | 2.6 | 12.4 | 3.3 | 1.3 | 13.1 |
| | Cwa | 55.9 | 2.4 | 4.2 | 1.4 | 0.6 | 1.2 | 0.4 | 5.6 | 7.7 | 3.4 | 17.2 |
| | Csc | 3.7 | 0.2 | 3 | 0.7 | 0.5 | 3.6 | 0.4 | 3.2 | 31.3 | 36.4 | 16.8 |
| | Csb | 51.1 | 0.9 | 0.1 | 8.8 | 0.2 | 4.6 | 2.4 | 5.6 | 17.3 | 7.9 | 1 |
| | Csa | 51.9 | 5.8 | 0.2 | 3.9 | 1 | 0.3 | 3.9 | 10.1 | 14.4 | 7.4 | 1.1 |
| | Cfc | 53.9 | 0.1 | 0.8 | 6.7 | 2.9 | 1.8 | 0.7 | 12.7 | 2.6 | 9.9 | 7.9 |
| | Cfb | 81.7 | 1.1 | 1.1 | 0.1 | 2.6 | 0.3 | 4.4 | 1.8 | 3 | 1.5 | 2.5 |
| | Cfa | 60.5 | 0 | 1.4 | 1.6 | 0.8 | 1 | 2.2 | 18.1 | 8.3 | 4.1 | 1.9 |
| Arid | BWk | 56.4 | 0 | 0.8 | 1.5 | 1.5 | 0.1 | 0.5 | 18 | 8.9 | 2.3 | 10 |
| | BWh | 56.6 | 1.6 | 0.4 | 5.9 | 0 | 6.3 | 0.5 | 3.4 | 20.5 | 1.5 | 3.3 |
| | BSk | 71.2 | 1.1 | 0.2 | 0.9 | 4.9 | 0.6 | 1.2 | 8.3 | 4.8 | 2.8 | 4.1 |
| | BSh | 77 | 6 | 0.4 | 2.9 | 3.4 | 2 | 0.5 | 3.7 | 2.5 | 0.2 | 1.4 |
| Tropics | Aw | 84.2 | 3.9 | 1.5 | 1.7 | 0.3 | 0.5 | 2.4 | 1.5 | 1.2 | 2 | 0.8 |
| | Am | 72.7 | 7 | 3.5 | 1.5 | 1.3 | 2 | 2.6 | 2.2 | 2.1 | 0.6 | 4.4 |
| | Af | 51.9 | 8.4 | 0.1 | 0.4 | 1 | 9.1 | 2.2 | 5 | 4.2 | 6.3 | 11.3 |

**Main climates**
A: Equatorial
B: Arid
C: Temperate
D: Snow
E: Polar

**Precipitation**
W: Desert
S: Steppe
f: Fully humid
s: Summer dry
w: Winter dry
M: Monsoonal

**Temperature**
h: Hot arid
k: Could arid
a: Hot summer
b: Warm summer
c: Cool summer
d: Extremely continental
F: Polar frost
T: Polar tundra

**Fig IV.6**.Partitioning of the variation in threatened species distribution in response to climate and land-use change. The variation is partitioned by each individual variable (X- axis) and in each subdivision of Köppen-Geiger climate classification (Y-axis) for all threatened species of reptiles, plants, mammals, amphibians and birds when explained by total species richness. Dark colors show higher variance explained by each variable. Cells with 0 show no threatened species exists in that particular subdivision of Köppen-Geiger climate zones.

## Discussion

We show that risks to threatened species distribution are widespread and are unlikely to act alone; but rather are spatially overlapped and jointly impact biological communities. Moreover, the importance of individual variables varies in each Köppen-Geiger climate classification, suggesting drivers of threatened species are not evenly distributed.

Among the ten threats we mapped, extreme climate events, standardized local anomalies and trends in temperature and precipitation are among four influential variables in almost all classes of Köppen-Geiger, suggesting the interactions of events and trends in the large part of the world. Intensification of extremes events can be a threat for individuals with life histories more sensitive to the duration and magnitude of climate events (Jentsch et al., 2007) and increase mortality in species (Coleman & Wernberg, 2020). Rising temperature (temperature trend) however, do not directly reduce niche availability for most of species but do trigger poleward or upward shifts for species living in their lower thermal limits and threaten the extinction of those living close to their upper climatic tolerance limit. However, little is known about the biodiversity response to climate trends when coupled with other associated drivers such as extreme events or high velocity of climate change (see Malhi et al., 2020).

In addition, climate has different parameters (e.g., temperature, precipitation, evapotranspiration, direction and speed of wind, etc.) and each parameters of climate change may also affect species in different way (Tingley et al., 2009); for example, our results show the precipitation in southern Chile, Myanmar, East India, Northern Philippines, and some west African countries have been substantially decreased over the last century. Experiments can casually link precipitation change to plant diversity change (Korell et al., 2021). However, how precipitation change, interacts with temperature and other threats such as land-use, requires more examination on a local and regional scale.

We also show, that climate is not acting in isolation, but rather interact with other human threats. For example, threatened species in Southeast Asia, in addition to the sever climate change (high extreme events, high standardized anomalies and trend), have been exposed to extremely high rate of deforestation and agricultural intensification. A recent study showed that the total mean annual forest cover loss during 2001-2019 was 3.22 Mha $yr^{-1}$, with 31% occurring in the mountains (Feng et al., 2021).

In general, our findings confirm previous findings (see Waldron et al., 2017) that high-risk areas of both climate and land-use change are among areas with a substantial decline in total global biodiversity (BDS score).

Tropics for example, is a known global hotspot of biodiversity and endemism, however, is also one of the hotspots of the highest risks from both climate and land-use change. Drivers that tend to be simultaneously present in the region are associated with extreme events, standardized local anomalies, gradual warming (trend), agricultural intensification and land frequency change.

It is important to note that our data are not comprehensive of all threats to all species. For example, our analysis does not take into account all human pressures (e.g., hunting, logging, industrial activities, pollution, etc) or invasive species and infectious diseases that have already impacted biodiversity worldwide (Allan et al., 2019; Harfoot et al., 2021). Our results are therefore conservative, and more species might be impacted than our maps indicates.

Quantifying the exposure of threatened species distribution and risks, does not necessarily imply that the threat is impacting all species in the same level. For example, not all species are at equal risk of climate change velocity (Davies et al., 2009). Strong disperses should be most able to maintain distributional equilibrium with climate condition and are therefore likely to occupy more of their potential range and avoid extinction (Sandel et al., 2011). Species with small ranges are at particular risk of extinction (Davies et al., 2009), because they often have small population sizes and densities and are less likely to occupy refuges that remain suitable during climate oscillations (Jansson, 2003; Ohlemller et al., 2008). However, when multiple stressors from climate, co-occur with sever land-use change (e.g., deforestation, unsustainable agriculture, logging, etc.) and cause fragmentation or reduction in quality of key habitat that would be a real challenge for species (WWF, 2020).

To our knowledge, we provide the first global assessment of multiple dimensions of climate change and land-use change as threats for biodiversity. The sum of these individual impacts is then mapped to show the cumulative anthropogenic influence, allowing visualization of the total impact of threats, which are often compounded by synergies and interactions (e.g., Evans et al., 2011).

Visualization of the spatial distribution of threats to species (threat maps) is highly recommended in systematic conservation planning for deciding which actions to take where and to prioritise limited resources (Margules & Pressey, 2000). Conservation planning is an inherently spatial process; therefore, explicitly considering the spatial dimension of threats could significantly enhance our ability to direct efforts to areas where the greatest conservation outcomes can be delivered.

Here we suggest that a far greater focus be placed on mapping the spatial distribution of different threats and considering how the cumulative impacts of threats to species vary across different locations and multiple spatial scales. Incorporating such a spatial context into future research will advance our understanding toward determining what mitigating actions we should take in a given location. In particular, disentangling Spatio-temporal threatening processes, and predictions of future threats to biodiversity should be a high priority for future research.

# SYNTHESIS

Species are on the move, often shifting, shrinking and expanding. The global reshuffling of biodiversity may provide opportunities for some species to spread but threaten others with extinction. Anthropogenic climate change, particularly warming temperature, is unequivocally known as the main culprit for these shifts. The reason is that historical range shifts are often correlated with geographic or climate gradients. When distributional shifts match expected gradients, it is assumed that climate change is the likely driver of such shifts. But there are classical problems of inference based on correlations because correlations do not necessarily imply causations. There are two potential problems with such an approach: i) pattern detection (how can one be sure that the observed patterns would not have arisen by chance?); ii) attribution (how can one be sure that the hypothesized drivers are the ones driving the observed pattern?).

Although, climate-driven range shifts are well documented (e.g., Parmesan et al., 1999; Thomas & Lennon, 1999; Virkkala & Lehikoinen, 2014) however, uncertainties associated with data and methods are typically unexplored.

This thesis explored these uncertainties and addressed questions related to the minimum standards that should be required to assess species range shifts under contemporary climate change.

In this final chapter, the most important results from the thesis are summarized together in order to better understand the key aspects of this thesis and to highlight the inter-relationship between them.

One of the key questions of this thesis is, how robust are data and methods associated with climate-related range shifts and whether these studies took in
account the full complexity of environmental changes? To answer this question, we reviewed 240 reports of climate-induced range shifts and evaluated the data, method and results using simple scoring criteria. The criteria revolved around i) pattern detection, ii) attribution and iii) reproducibility of the reports Chapter (I) (Box 1).

The results revealed that only a minority of the studies matched the scientific criteria we proposed here. The findings showed that most of the reports are univariate (focusing on temperature) and unidirectional (focusing on poleward or upward shifts).

This chapter proved that data documenting climate change effects on species distribution is geographically biased and mainly restricted to the northern hemisphere, almost no empirical data exists for the tropics, and data for the ocean is largely missing. Despite some improvements in the data and methods used in reports of climate-induced range shifts, substantial scope exists for raising standards. This chapter provided a hint of the best practice-standards needed to assess the impact of anthropogenic climate change on species range shifts.

We used the minimum standards (scoring criteria) proposed in the Chapter (I) to detect range shifts in 85 British Breeding Bird and attribute these shifts to climate and land-use change Chapter (II).

This chapter particularly asked whether observed range shifts in bird species were best explained by climate or land-cover change; or whether they are not distinguishable from what would be expected by chance (null model)?

Our findings implied that different mechanisms were likely to shape bird's species range dynamics in Great Britain and the importance of such mechanisms are not evenly distributed across sections of species range.

For example, range shifts in the southern margins (rear edge) of northerly distributed species in Great Britain were best explained by climate change, while shifts across the northern margins (leading edge) of southerly distributed species were best explained by land-use change. In contrast, at the northern and southern edges of Great Britain range dynamics could not be distinguished from that expected by chance, suggesting the effect of boundary limiting the direction and magnitude of range shifts.

These results reinforce the view that comprehensive assessments of climate change effects on species range shifts needs to examine alternative drivers of change in equal footing.

As stated earlier in Chapter (I) the empirical research linking climate change to biodiversity dynamics is univariate and using single metrics of climate change (e.g., simple anomalies). However, evidence suggests single metrics would not capture the wider range of effects captured by multiple metrics (e.g., Garcia et al., 2014) and may underestimate the true level of climate change (e.g., VanDerWal et al., 2013).

One reason for limited exploration of climate change manifestations in climate-change-induced biodiversity impact assessments is that no convenient platform exists where all commonly used metrics are implemented. Moreover, the existing tools to quantify the metrics are scattered, substantially different in the way they handle spatio-temporal data, their input and output, and the degree of being user friendly.

To fill this gap, “*Climetrics*” R package (Chapter III) was developed. The “*Climetrics*” package can handle large spatio-temporal raster datasets and contains six commonly used climate change metrics including: 1) Standardized local anomalies; 2) Changes in probability of local climate extremes; 3) Change in area of analogous climates; 4) Novel climates; 5) Change in the distance to analogous climates; and 6) Climate change velocity.

The “*Climetrics*” R package should provide a set of useful tools to map the complexity in climate change using multivariate climate parameters and more sophisticated methods rather than simple anomalies used in most of studies.

Chapter (IV) was inspired by Chapter (I), Chapter (II) and Chapter (III) and delved deeper into the environmental complexity that may increase extraction risk for threatened species. It should be pointed out, that this chapter did not aim to detect changes in species distribution or find correlations and causations, but to map the global distribution of risks associated with complexity in climate and land-use change. The Chapter used a comprehensive characterization of historical climate and land-use changes during the 20th century and mapped ten risks from five climate change metrics and five land-use transitions. Then compared the ensuing patterns with diversity patterns among the global distribution of threatened amphibians, birds, mammals, reptiles, and plant species. The maps for multiple dimensions of climate change were generated using the “*Climetrics*” R package which was developed in Chapter (III). The results showed risks associated with multiple dimensions of climate and land-use change are widespread and are unlikely to act alone; rather are spatially overlapped and jointly impact biological communities. In addition, risks of both climate and land use are not evenly distributed across the different climatic zones. The founding of Chapter (II) also confirmed that different mechanisms are affecting species in different sections of the distribution.

Explaining the idiosyncratic nature of range shifts is an urgent question that we cannot fully assess using these existing methods. In order to formally detect and attribute a biological response to anthropogenic drivers, first, one needs to demonstrate that the system affected has changed in some significant statistical sense (change detection); or whether observed patterns in any given response variable could have arisen by chance, and secondly, determine the relative contribution of multiple causal factors to the change with an assignment of statistical confidence (attribution)(see Taheri et al., 2016).

Despite the remarkable number of climate-related range shift studies, no best practice standards exist for these assessments. The lack of standard measurements, causes considerable uncertainties regarding the magnitude, direction and drivers of distributional shifts (e.g., VanDerWal et al., 2013; Yalcin & Leroux, 2018).

Without understanding the fundamental drivers of range edges, it is impossible to reliably predict how they will respond to future climate change (La Sorte & Jetz, 2012).

# CONCLUSIONS

This thesis offers some key perspectives in which are highlighted as follows:

- Understanding range dynamics and their underlying causes thus require a more sophisticated analysis than is typically performed. This thesis highlights the need for best-practice standards for assessments of climate-related range shift studies.

- Seeking to attribute climate change to given distributional shifts is thus better achieved by relating species range change with climate variables instead of geographical proxies, such as latitude and elevation.

- Moreover, Climate is a multivariate phenomenon. Not only it involves different parameters, like temperature, precipitation, and wind, but it also expresses itself at different geographical extent and temporal scales. Adequately capturing the wealth of climate change manifestations and the different ways it interacts with the living systems requires that its multiple dimensions be appropriately characterised through alternative, often orthogonal, metrics
- In addition, even when climate change variables are used, instead of geographical proxies, to examine relationships with species

distributional shifts, there are occasions when distributional shifts respond not only to climate but also to other environmental

changes, such as spread of disease or land-use change. Attributing a mechanism to an observed pattern thus benefits from examination of multiple alternative hypotheses on equal footing. However, multifaceted inference was found to be extremely rare in the reviewed literature.

- The thesis also reinforces the use of null models to assess whether observed pat- terns could have arisen by chance alone.

- The thesis also showed different mechanisms are likely implicated in shaping species range dynamics and the importance of different variables varies across sections of species ranges.

- The thesis also provides evidence that threats to biodiversity are widespread and are unlikely to act alone; but rather are spatially overlapped and jointly impact biological communities. Suggesting a far greater focus should be placed on mapping the spatial distribution of different threats and considering how the cumulative impacts of threats to species vary across different locations and multiple spatial scales.

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# APPENDIX A. CHAPTER I

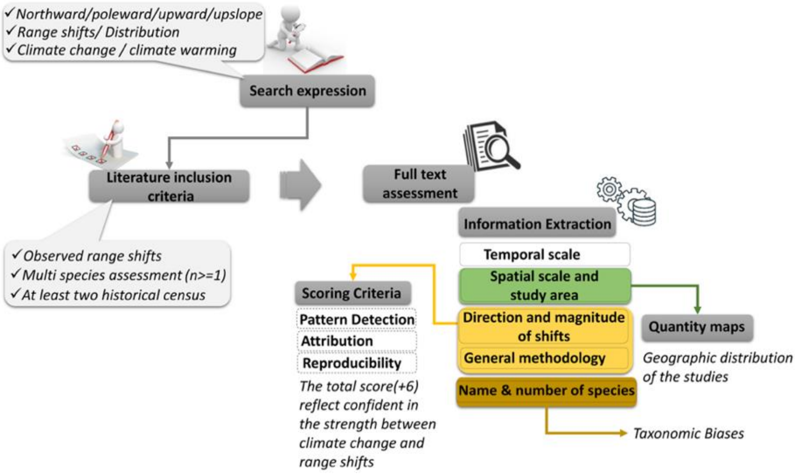


**Fig A-2** 1.General methodological framework. Shows the overall process in reviewing climate- related range shifts studies.

**Table A-1** 1.Detailed information about articles (e.g., Time period, Magnitude of range shifts duration, Ecosystem and Climate zone of study area, Temperature change during the study period, Causal factors tested, Type of specie strait, etc.) and detailed criteria scoring for all 240 articles. Available in GitHub repository

(https://github.com/Shirin-t/SciAdv-2/blob/main/abe1110_table_s1.xlsx).

**Table A-1 2**.List of species from published articles (Duplicated names are removed). Available in GitHub repository

(https://github.com/Shirin-t/SciAdv-2/blob/main/abe1110_table_s2.xl

# APPENDIX B. CHAPTER II

## Discriminating climate, land-cover and random effects on species range dynamics

## Method:

### Interaction effect of climate and land-cover change

We used linear regression to measure the relative importance of all hypothesized predictors of range shifts (climate and land cover) and their possible interactions at the leading of southerly distributed (n=47), and rear edges of northerly distributed and northerly distributed species (n=35). We considered species range shifts as the response variable (Y) and land-cover/climate change as predictor variables (X) (Figure S1).

First, we selected the 20 most marginal records in the northern and southern boundary of the distribution and then calculated the average latitudinal shifts in the species ranges between these marginal cells in $t_2$ or $t_3$ minus $t_1$ (baseline). In order to determine the strength of the signals from land-cover and climate in observed range shifts across the margins of species distributions, we first, extracted and averaged the values of each land-cover and climate variables in the 20 most marginal records at the leading and rear edge for each species and in the two time slices considered ($t_1$ and $t_2$ or $t_3$). Then, we subtracted the average value of climate or land-cover in the second time $t_2$ or $t_3$) from the same variable in the baseline ($t_1$). After applying this, we obtained a table which contains the observed magnitude of range shifts and the average magnitude of three climates (Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month, Total Annual Precipitation) and six land-cover variables (proportion of Settlements, crop-lands, forest-cover, grasslands, other-lands and water within each cell) for each species. We ran the linear regression to assess if interaction effects are detected between climate and land-cover variables in explaining latitudinal range shifts. Prior to analyzing the data, we checked for data collinearity by calculating the variance inflation factor (VIF). We repeated this procedure for each geographical section of the distributions and removed collinear variables (VIF >10). The multicollinearity test detected a high inverse correlation between croplands and grasslands in the species ranges, and due to the high value of the Variance Inflation Factor (VIF), cropland was excluded from the regression model in both time slices (t1 vs. t2 and t1 vs. t3).

In order to find the possible interaction effects between climate and land-cover variables, we did a factorial design in which we regressed only one variable of climate at a time and crossed with land-cover variables, so there are results for each of the 3*6 combinations of levels (Figure S1). All analysis were performed in RStudio Version 1.2.5019.

## Results

The analysis of variance (ANOVA) showed the importance of both climate and land-cover change to determine range shifts across different sections of the species range. Among the different linear models, we tested, we also found four significant interactions in which land-cover change interact with climate change variables to determine the latitudinal species range shifts.

At the leading edge of the southerly-distributed species between t1 and t2, the analysis of variance (ANOVA) showed that the range shifts are better explained by grasslands and Maximum temperature during the breeding season ($P < 0.001$). Open-lands (e.g., pasture and bare soil) ($P < 0.01$) and water bodies (e.g., Sea, streams) ($P < 0.05$) also showed a significant contribution ($P < 0.05$) (Table B.3.1). The analysis of ANOVA in the second time slice (t1 vs. t3) showed that maximum temperature remained important variable ($P < 0.01$), followed by grasslands, forest-cover ($p <0.001$) and urban areas ($p <0.05$) explained some variation in shifts in this section of the distribution (Table B-3 1).

In this section of the distribution, we found evidence for the interaction effect between land-cover change (open-lands and grasslands) and climate change conditions (minimum and maximum temperature) on species range shifts (Figure S2 a,b). The interaction plot shows that the relationship between range shifts and minimum temperature depends on the loss (-) and gain (+) of open-lands ($p < 0.001$). Meaning, when the open-land value is at its low (-) the magnitude of range shifts caused by minimum temperature is higher than when open-land is at its high (+), this interaction effect was consistent during the 20 years ($P < 0.001$; Fig B-3 2.a) and 40 years ($P < 0.001$; Fig B-3 2.a).

At the leading edge of southerly-distributed species, we found another significant interaction effect between maximum temperature and grasslands during the 20 years (t1 vs. t2). The interaction plot shows that grassland loss (-) interacts with maximum temperature and accelerate the northward movement (Fig B-3.2b). Conversely, gaining grasslands (+) in interaction with maximum temperature cause southward shifts (Fig B-3.2b). The interaction plot in the second time slice (t1 vs. t3), suggests a significant interaction effect between maximum temperature and forest-cover ($P = 0.002$; Figure S2.b). Meaning, forest loss (-) interacts with maximum temperature and move the leading edge of southerly-distributed species further to the north. Conversely, forest gain (+) in interaction with maximum temperature cause southward shifts in this section of the distribution.

At the rear edge of northerly-distributed species, rang shifts significantly explains by minimum temperature ($p < 0.001$) (Table B-3 1).

At this section of the distribution, we found a significant interaction between minimum temperature and forest cover (Figure B-3 2.c, B-3 3.c), for both time slices (t1 vs t2 & t1 vs. t3). The interaction plot suggests forest loss (-) interacts with maximum temperature and cause shifts toward higher latitude, while gaining forest (+) in interaction with maximum temperature causes shifts toward south (Fig B-3 2.c).

Our analysis detected another interaction effect between maximum temperature and urban area ($P < 0.001$). The interaction plot shows, gaining urban areas, interact positively with precipitation and cause that the rear edge of northerly distributed species moves toward north during the breeding season, while loss urbanization between two times cause shifts toward south (Fig B-3.2 b. d) .

In the second time slice (t1 vs t3) we detected a significant interaction effect between precipitation and open lands ($P = 0.003$). The interaction plot suggests that when open lands is at its high (+) maximum temperature cause that rear edge of northerly distributed species move toward south, while open-lands loss in interaction with maximum temperature cause northward shifts.

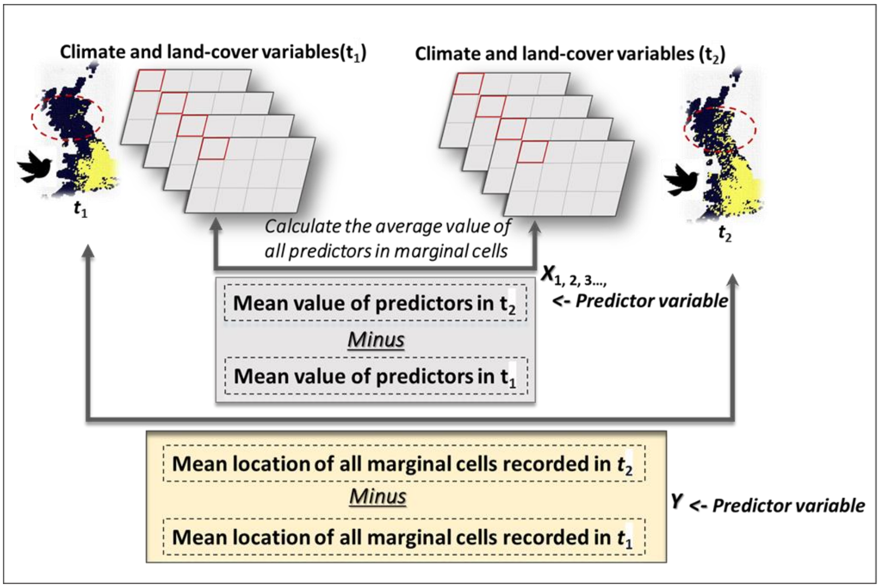


**Fig B-3 1.** Flowchart showing the methodological steps used for analysis of finding interaction between predictors

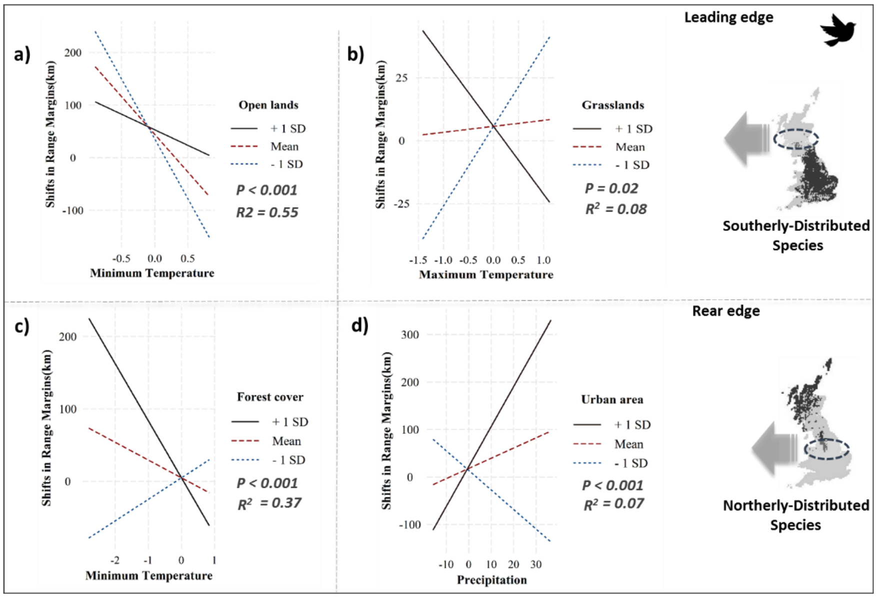


**Fig B-3 2**. Interaction effect between climate and land-cover predictors among leading (a,b) edges of southerly distributed species (n=47), and rear edges (c,d) of northerly distributed species(n=35). The crossed line on the graph suggest the interaction effect among two predictors between (1968-72 and 1988-91). The significant interaction detected between, a) minimum temperature and open-lands, b) maximum temperature and Grasslands at the leading edge of southerly-distributed species, c) minimum temperature and forest-cover and d) precipitation and urban are at the rear edge of northerly-distributed species. The response variable on the vertical y-axis (range shifts) and a response variable in the x-axis (minimum/ maximum temperature). The three lines in the legend shows mean of the moderator in red and standard deviation below and above the mean (+/- SD).

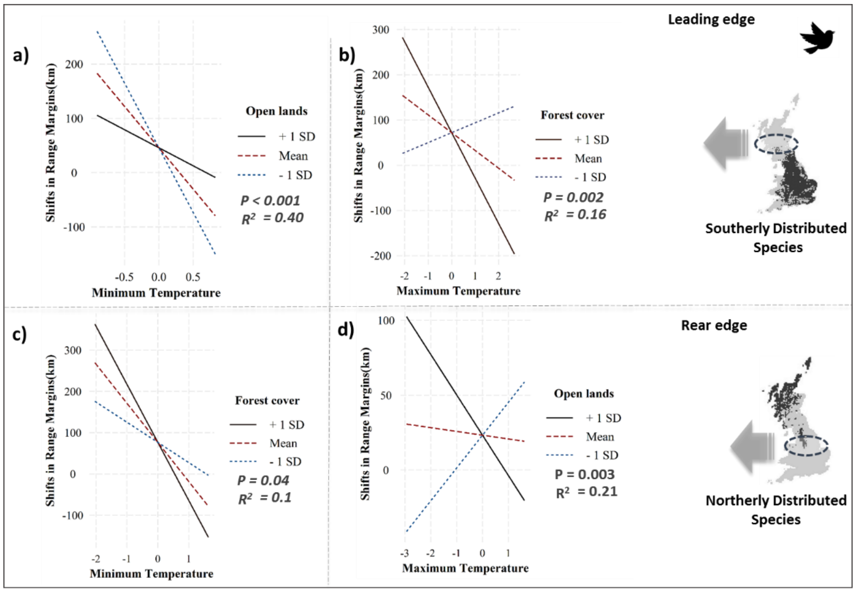


**Fig B-3 3**. Interaction effect between climate and land-cover predictors among leading (a,b) edges of southerly distributed species (n=47), and rear edges (c,d) of northerly distributed species(n=35). The crossed line on the graph suggest the interaction effect among two predictors between (1968-72 and 2007-11). The significant interaction detected between, a) minimum temperature and open-lands, b) maximum temperature and Grasslands at the leading edge of southerly distributed species, c) minimum temperature and forest cover and d) maximum temperature and open lands at the rear edge of northerly distributed species. The response variable on the vertical y-axis (range shifts) and a response variable in the x-axis (minimum/ maximum temperature). The three lines in the legend shows mean of the moderator in red and standard deviation below and above the mean (+/- SD).

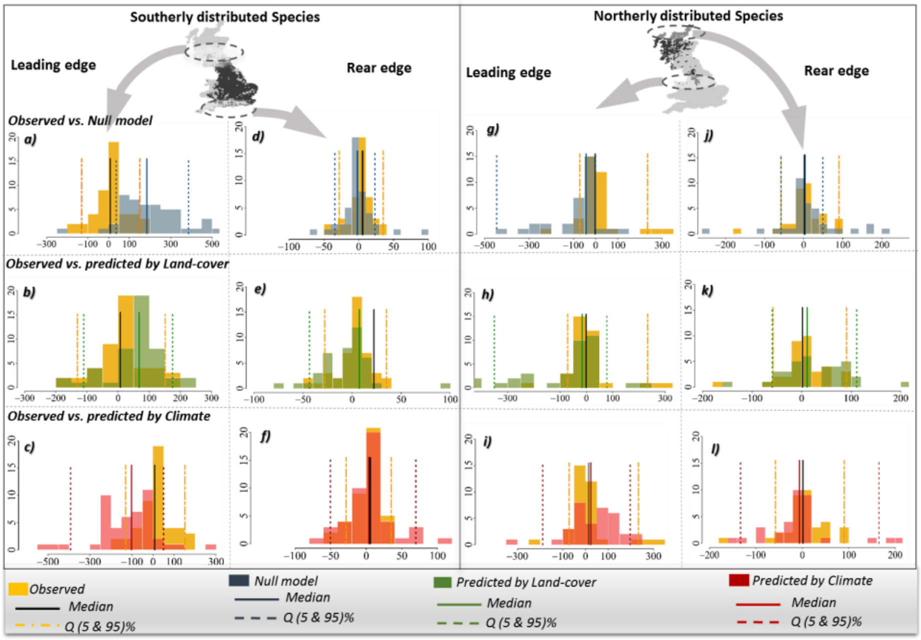


**Fig B-3 4**. Overlay histograms compare the distribution of observed latitudinal range shifts (yellow) with null model (blue), range shifts predicted by land-cover (green) and predicted by climate (red) between (1968-72 and 1988-91), among leading (a,b,c) and rear (d,e,f) edges of southerly distributed species (n=47), and rear (g,h,i) and leading edges (j,k,l) of northerly distributed species (n=35). The X-axis are intervals that show the range shifts, positive values means shifts toward north and negative values shows shifts toward south. The Y-axis implies the frequency of distribution within the interval set by the X-axis. The vertical dashed lines show the (5 & 95) % quantiles and the solid vertical lines show the median for observe and three alternative models. The y-axis shows the frequency of range shifts (distribution of latitudinal shifts by individual species along the different sections of the species distribution) and x-axis shows shifts in mean latitude for observed vs. three alternative models. Positive values in the x-axis indelicate northward shifts and negative values indicate the southward shifts.

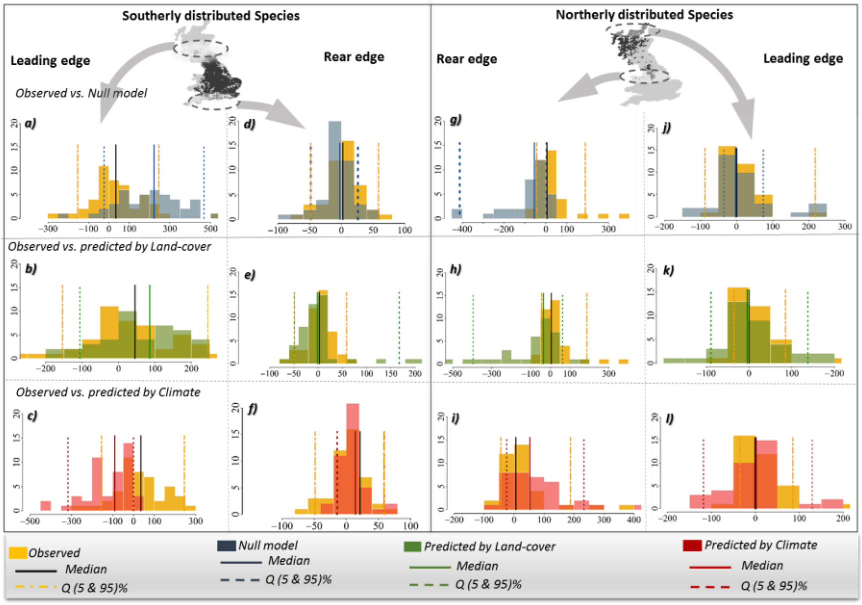


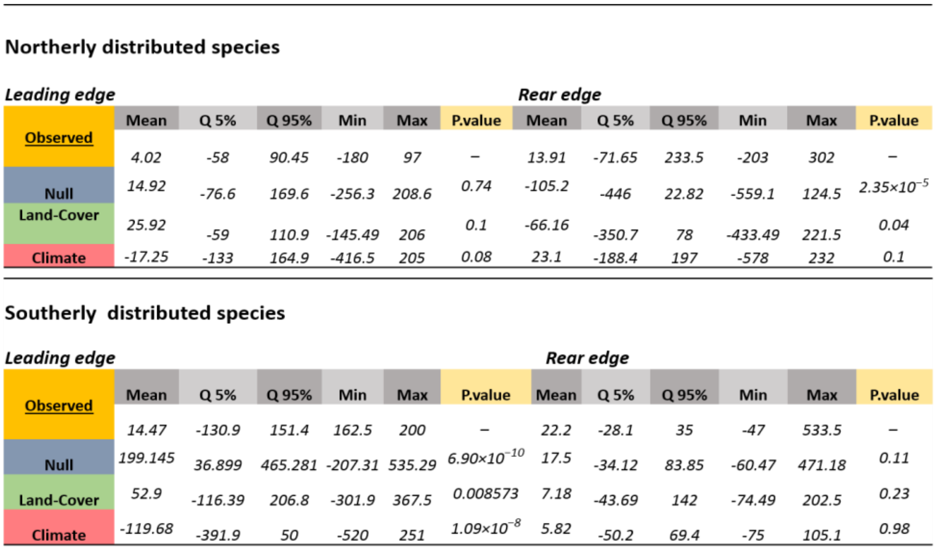
**Fig B-3 5.** Overlay histograms compare the distribution of observed latitudinal range shifts (yellow) with null model (blue), range shifts predicted by land-cover (green) and predicted by climate (red) between (1968-72 and 2007-11) among leading (a,b,c) and rear (d,e,f) edges of southerly distributed species (n=47), and rear (g,h,i) and leading edges (j,k,l) of northerly distributed species (n=35). The X-axis are intervals that show the range shifts, positive values means shifts toward north and negative values shows shifts toward south. The Y-axis implies the frequency of distribution within the interval set by the X-axis. The vertical dashed lines show the (5 & 95) % quantiles and the solid vertical lines show the median for observe and three alternative models. The y-axis shows the frequency of range shifts (distribution of latitudinal shifts by individual species along the different sections of the species distribution) and x-axis shows shifts in mean latitude for observed vs. three alternative models. Positive values in the x-axis indelicate northward shifts and negative values indicate the southward shifts.

| Leading edge of Southerly distributed species | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| $t_1$ vs. $t_2$ | | | | | | $t_1$ vs. $t_3$ | | | | |
| | Estimate | Std. Error | t value | Pr(>\|t\|) | | Estimate | Std. Error | t value | Pr(>\|t\|) | |
| (Intercept) | -7.649 | 15.560 | -0.492 | 0.205 | | 151.330 | 22.329 | 6.777 | 0.000 | *** |
| Urban area | 15.811 | 306.147 | 0.052 | 0.011 | * | 800.272 | 267.112 | 2.996 | 0.005 | ** |
| Grasslands | -62.420 | 85.474 | -0.730 | 0.000 | *** | 242.697 | 69.100 | 3.512 | 0.001 | ** |
| Open-lands | 296.414 | 620.554 | 0.478 | 0.003 | ** | -78.468 | 352.309 | -0.223 | 0.825 | |
| Water-bodies | -26.038 | 312.584 | -0.083 | 0.019 | * | -714.069 | 278.691 | -2.562 | 0.014 | * |
| Forest-cover | 130.189 | 181.294 | 0.718 | 0.004 | ** | 353.715 | 128.418 | 2.754 | 0.009 | ** |
| Min.temp | -34.556 | 30.108 | -1.148 | 0.36648 | | -19.692 | 25.554 | -0.771 | 0.446 | |
| Max.temp | -141.575 | 25.691 | -5.511 | 1.68E-07 | *** | -214.155 | 19.674 | -10.885 | 0.000 | *** |
| Precipitation | -1.639 | 0.942 | -1.741 | 0.033 | | -2.116 | 0.798 | -2.652 | 0.012 | |
| Residual standard error: 48.97 on 38 degrees of freedom. Multiple R-squared: 0.6723, Adjusted R-squared: 0.6033 F-statistic: 9.744 on 8 and 38 DF, p-value: 3.139e-07 | | | | | | Residual standard error: 48.54 on 38 degrees of freedom, Multiple R-squared: 0.8977, Adjusted R-squared: 0.8761, F-statistic: 41.66 on 8 and 38 DF, p-value: < 2.2e-16 | | | | |

**Table B-3 1.** Analysis of variance using all variables but cropland. The response variable is the average of range shifts at the leading edge of southerly-distributed species (t1 vs. t2 & t1 vs. t3) and predictor variables are the difference between the northern most marginal cells. Predictor variables included are as following: urban area, forest, grasslands, open spaces (e.g., glaciers, sparsely vegetated areas bare soil), maximum temperature in the warmest month, and minimum temperature in the coldest month and precipitation during the breeding season. ***, ** and * indicates if there is any significance difference and shows (p<0.001), (p<0.01) and (0.05) respectively. And shows (p<0.001), (p<0.01) and (0.05) respectively.

| **Rear edge of northerly-distributed species** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $t_1$ vs. $t_2$ | | | | | $t_1$ vs. $t_3$ | | | | |
| | Estimate | Std. Error | t.value | Pr(>\|t\|) | | Estimate | Std. Error | t value | Pr(>\|t\|) | |
| (Intercept) | 38.257 | 17.040 | 2.25 | 0.03 | * | 135.211 | 35.731 | 3.78 | 0.00 | *** |
| Urban area | -67.718 | 262.267 | -0.26 | 0.80 | | 243.330 | 208.850 | 1.17 | 0.25 | |
| Grasslands | -80.618 | 110.445 | -0.73 | 0.47 | | -72.526 | 51.927 | -1.40 | 0.17 | |
| Open-lands | -359.409 | 766.632 | -0.47 | 0.64 | | -623.430 | 432.016 | -1.44 | 0.16 | |
| Forest-cover | -417.778 | 357.400 | -1.17 | 0.25 | | -155.852 | 212.492 | -0.73 | 0.47 | |
| Water-bodies | -188.460 | 289.150 | -0.65 | 0.52 | | -88.483 | 206.068 | -0.43 | 0.67 | |
| Max.temp | 9.075 | 37.415 | 0.24 | 0.81 | | 3.743 | 26.312 | 0.14 | 0.89 | |
| Min.temp | -144.921 | 23.716 | -6.11 | 0.00 | *** | -151.773 | 17.682 | -8.58 | 0.00 | *** |
| Precipitation | 0.397 | 0.921 | 0.43 | 0.67 | | 0.007 | 0.991 | 0.01 | 0.99 | |
| Residual standard error: 42.69 on 26 degrees of freedom, Multiple R-squared: 0.8342, Adjusted R-squared: 0.7832, F-statistic: 16.35 on 8 and 26 DF, p-value: 2.43e-08 | | | | | | Residual standard error: 39.35 on 25 degrees of freedom, Multiple R-squared: 0.8449, Adjusted R-squared: 0.7891, F-statistic: 15.14 on 9 and 25 DF, p-value: 4.658e-08 | | | | |

**Table B-3 2.** Analysis of variance using all variables but cropland. The response variable is the average of range shifts at the leading edge of southerly-distributed species (t1 vs. t2 & t1 vs. t3) and predictor variables are the difference between the northern most marginal cells. Predictor variables included are as following: urban area, forest, grasslands, open spaces (e.g., glaciers, sparsely vegetated areas bare soil), maximum temperature in the warmest month, and minimum temperature in the coldest month and precipitation during the breeding season. ***, ** and * indicates if there is any significance difference and shows (p<0.001), (p<0.01) and (0.05) respectively. And shows (p<0.001), (p<0.01) and (0.05) respectively.



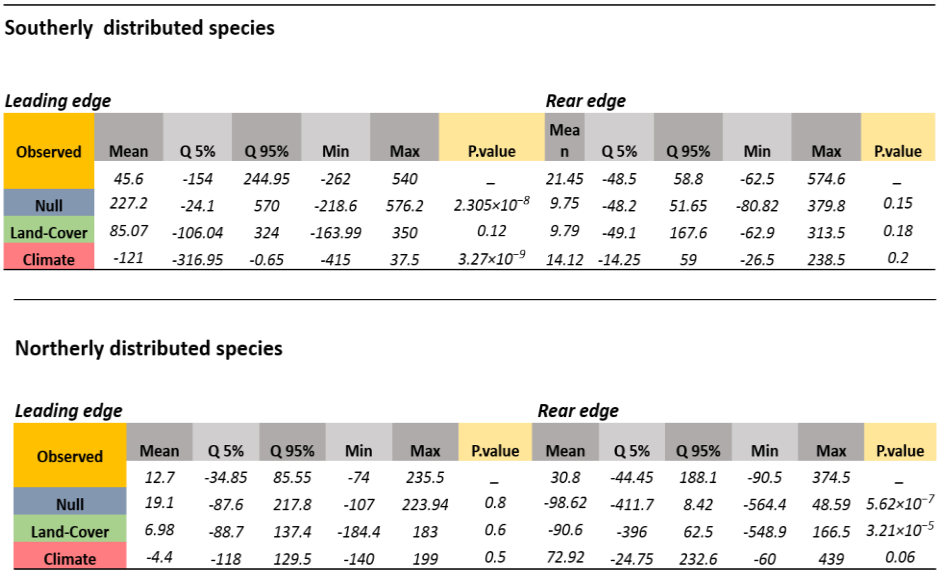
**Northerly distributed species**

| | *Leading edge* | | | | | | *Rear edge* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | Q 5% | Q 95% | Min | Max | P.value | Mean | Q 5% | Q 95% | Min | Max | P.value |
| Observed | 4.02 | -58 | 90.45 | -180 | 97 | – | 13.91 | -71.65 | 233.5 | -203 | 302 | – |
| Null | 14.92 | -76.6 | 169.6 | -256.3 | 208.6 | 0.74 | -105.2 | -446 | 22.82 | -559.1 | 124.5 | $2.35\times10^{-5}$ |
| Land-Cover | 25.92 | -59 | 110.9 | -145.49 | 206 | 0.1 | -66.16 | -350.7 | 78 | -433.49 | 221.5 | 0.04 |
| Climate | -17.25 | -133 | 164.9 | -416.5 | 205 | 0.08 | 23.1 | -188.4 | 197 | -578 | 232 | 0.1 |

**Southerly distributed species**

| | *Leading edge* | | | | | | *Rear edge* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | Q 5% | Q 95% | Min | Max | P.value | Mean | Q 5% | Q 95% | Min | Max | P.value |
| Observed | 14.47 | -130.9 | 151.4 | 162.5 | 200 | – | 22.2 | -28.1 | 35 | -47 | 533.5 | – |
| Null | 199.145 | 36.899 | 465.281 | -207.31 | 535.29 | $6.90\times10^{-10}$ | 17.5 | -34.12 | 83.85 | -60.47 | 471.18 | 0.11 |
| Land-Cover | 52.9 | -116.39 | 206.8 | -301.9 | 367.5 | 0.008573 | 7.18 | -43.69 | 142 | -74.49 | 202.5 | 0.23 |
| Climate | -119.68 | -391.9 | 50 | -520 | 251 | $1.09\times10^{-8}$ | 5.82 | -50.2 | 69.4 | -75 | 105.1 | 0.98 |

**Table B-3 2**. Statistical results for the observed range shifts and range shifts modelled by three alternative models between (1967-72 and 1988-91) for leading and rear edge of northerly and southerly-distributed species. The table shows the mean of range shifts, quantile 5%, quantile 95%, minimum and maximum value of range shifts and the p-value (Wilcoxon signed-rank test compares observed range shifts with three alternative models).



Southerly distributed species

| | Leading edge | | | | | | Rear edge | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Observed | Mean | Q 5% | Q 95% | Min | Max | P.value | Mean | Q 5% | Q 95% | Min | Max | P.value |
| | 45.6 | -154 | 244.95 | -262 | 540 | – | 21.45 | -48.5 | 58.8 | -62.5 | 574.6 | – |
| Null | 227.2 | -24.1 | 570 | -218.6 | 576.2 | $2.305\times10^{-8}$ | 9.75 | -48.2 | 51.65 | -80.82 | 379.8 | 0.15 |
| Land-Cover | 85.07 | -106.04 | 324 | -163.99 | 350 | 0.12 | 9.79 | -49.1 | 167.6 | -62.9 | 313.5 | 0.18 |
| Climate | -121 | -316.95 | -0.65 | -415 | 37.5 | $3.27\times10^{-9}$ | 14.12 | -14.25 | 59 | -26.5 | 238.5 | 0.2 |

Northerly distributed species

| | Leading edge | | | | | | Rear edge | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Observed | Mean | Q 5% | Q 95% | Min | Max | P.value | Mean | Q 5% | Q 95% | Min | Max | P.value |
| | 12.7 | -34.85 | 85.55 | -74 | 235.5 | – | 30.8 | -44.45 | 188.1 | -90.5 | 374.5 | – |
| Null | 19.1 | -87.6 | 217.8 | -107 | 223.94 | 0.8 | -98.62 | -411.7 | 8.42 | -564.4 | 48.59 | $5.62\times10^{-7}$ |
| Land-Cover | 6.98 | -88.7 | 137.4 | -184.4 | 183 | 0.6 | -90.6 | -396 | 62.5 | -548.9 | 166.5 | $3.21\times10^{-5}$ |
| Climate | -4.4 | -118 | 129.5 | -140 | 199 | 0.5 | 72.92 | -24.75 | 232.6 | -60 | 439 | 0.06 |

**Table B-3 3**. Statistical results for the observed range shifts and range shifts modeled by three alternative models between (1968-72 and 2007-11) for leading and rear edge of northerly and southerly-distributed species. The table shows the mean of range shifts, quantile 5%, quantile 95%, minimum and maximum value of range shifts and the p-value (Wilcoxon signed-rank test compares observed range shifts with three alternative models).

**Table B-3 4& Table B-3 5**. show shifts in species ranges based on observe, climate model, land-cover-based and null model, for each individual species and first (Table S5; t1 vs t2) and second time (Table S6; t1 vs. t3) slice respectively. Both table contains, scientific name of species, number of occupied cells in the first time (Occ.t1), number of occupied cells in the second time (Occ.2), Occupancy change between two times (Log10 (occupancy-t2/occupancy-t1), distributional range of species (N=Northerly vs. S=southerly), observed range shifts in leading and trailing edge (Obs-Leading edge & Obs-Rear edge), shifts modelled by null (Null-Leading edge & Null-Rear edge), land-cover(Lnd-Leading edge & Lnd-Rear edge) and climate (Clim-Leading edge & Clim-Rear edge) for both leading and rear edges. (Tables are in the next page).

# TableB-3 5

| Species-Name | Occ.t1 | Occ.t2 | Occupancy | Range | Obs-Leadin | Obs-Rear e | Null-Leadir | Null-Rear e | Lnd-Leadin | Lnd-Rear e | Clim-Leadi | Clim-Rear edge |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Accipiter_nisus | 1823 | 2178 | 0.077271 | S | 22 | 1 | 211.54 | 5.94 | 69.5 | 12.5 | -59.5 | 18 |
| Acrocephalus_palustris | 21 | 15 | -0.14613 | S | -1 | 11.5 | 227.81 | 98.31 | 55.34 | 150.84 | 47.67 | 61.17 |
| Acrocephalus_scirpaceus | 775 | 790 | 0.008325 | S | 100.5 | -5.5 | 492.28 | -2.26 | 161.5 | 3.5 | -7.5 | -21.5 |
| Actitis_hypoleucus | 1406 | 1424 | 0.005525 | N | 42 | -59.5 | 43.28 | -63.52 | 90.5 | -57 | -97.5 | 73 |
| Alcedo_athis | 1305 | 1224 | -0.02783 | S | 53.5 | 1.5 | 295.91 | -2.14 | 85 | -9 | -164 | 2.5 |
| Alectoris_rufa | 919 | 1214 | 0.120903 | S | 97.5 | -13 | 312.59 | -21.41 | 26.5 | -39.5 | -243.5 | -7.5 |
| Anas_acuta | 86 | 85 | -0.00508 | N | -33.5 | -8 | -52.38 | -30.67 | -45 | 1.5 | -42 | -22.5 |
| Anas_clypeata | 520 | 454 | -0.05895 | S | 91.5 | -5.5 | 57 | -9.82 | -73 | -23 | -105 | -57 |
| Anas_crecca | 1376 | 1146 | -0.07943 | N | 52 | 19 | 22.13 | -17.01 | 44.5 | 18.5 | -130 | 189.5 |
| Anas_penelope | 283 | 360 | 0.104516 | N | 45 | -39.5 | 24.47 | -66.25 | 62.5 | 20 | 3.5 | -89.5 |
| Anas_querquedula | 136 | 138 | 0.00634 | S | 167 | 35 | 349.25 | 22.62 | 59 | 12.5 | -33 | -25.5 |
| Anas_strepera | 158 | 357 | 0.354011 | S | 113.5 | -30.5 | 239.36 | -41.33 | 68.5 | -56 | -63.5 | -75 |
| Anser_anser | 200 | 718 | 0.555094 | N | 91.5 | -64 | 139.52 | -126.46 | 112 | -31.5 | 205 | -123 |
| Anthus_trivialis | 1793 | 1524 | -0.0706 | S | -3 | -5 | 104.38 | -6.62 | 41 | -1 | -26 | 25.5 |
| Ardea_cinerea | 1686 | 2335 | 0.141429 | N | 97 | -14.5 | 208.68 | -21.24 | 84 | 7.5 | -38 | 37 |
| Asio_flammeus | 800 | 679 | -0.07122 | N | -5.5 | -8 | 26.6 | -91.82 | 92.5 | -87.5 | 11.5 | 123 |
| Asio_otus | 590 | 445 | -0.12249 | N | -55 | 8.5 | 36.17 | -22.15 | -52 | -17 | -87 | 4.5 |
| Athene_noctua | 1381 | 1228 | -0.051 | S | -19.5 | 21 | 341.99 | 16.28 | 119 | 3.5 | -102.5 | 18.5 |
| Aythya_ferina | 512 | 511 | -0.00085 | S | 29.5 | -2 | 142.73 | -9.23 | 11 | -19.5 | -83 | -8 |
| Aythya_fuligula | 1290 | 1484 | 0.060844 | S | 22.5 | -21 | 72.45 | -30.65 | -121.5 | -28.5 | -207.5 | 3.5 |
| Caprimulgus_europeaeus | 562 | 274 | -0.31199 | S | -161.5 | 15 | 122.33 | 15.4 | -35 | 21.5 | -228 | -14.5 |
| Carduelis_cabaret | 1979 | 1754 | -0.05242 | N | 8.5 | -4.5 | 92.47 | -23.95 | 53 | -9.5 | -22 | 85.5 |
| Carduelis_flavirostris | 656 | 651 | -0.00332 | N | 1.5 | -26 | -6.1 | -278.37 | -13.5 | -277 | -0.5 | 191 |
| Carduelis_spinus | 625 | 1158 | 0.267829 | N | 22.5 | -39.5 | 166.02 | -74.06 | 90.5 | -34.5 | 10.5 | 59 |
| Charadrius_dubius | 288 | 420 | 0.163857 | S | 34.5 | -47 | 450.53 | -60.48 | 98.5 | -74.5 | 51 | -46 |
| Cinclus_cinclus | 1434 | 1309 | -0.03961 | N | -2 | -1.5 | 46.24 | -4.14 | 70.5 | 20 | -8.5 | 44.5 |
| Coccothraustes_coccothraustes | 459 | 315 | -0.1635 | S | 7 | 4 | 241.25 | -2.25 | 54.5 | -27 | -231 | -8 |
| Columba_livia | 1498 | 2085 | 0.143594 | N | -2 | -5 | -0.02 | -6.74 | -1.5 | 13.5 | 3 | -12 |
| Columba_orenas | 1956 | 1821 | -0.03106 | S | -16 | 6 | 151.88 | -2.15 | 35 | 8.5 | -29.5 | 2.5 |
| Corvus_corax | 1243 | 1130 | -0.04139 | N | 2 | 0.5 | -5.41 | -0.16 | 4 | 24 | -0.5 | -6.5 |
| Coturnix_coturnix | 405 | 804 | 0.297801 | S | 200 | 0 | 225.38 | -1.38 | 50.5 | 0 | -433.5 | -22.5 |
| Crex_crex | 659 | 161 | -0.61206 | N | -65 | 302 | -109.71 | 64.81 | -32.5 | 154 | -97.5 | 232 |
| Dendrocopus_minor | 889 | 790 | -0.05127 | S | -3.5 | 21 | 471.61 | 13.23 | 209.5 | 0 | -95.5 | 18 |
| Emberiza_calandra | 1357 | 921 | -0.16832 | S | -131.5 | 29 | -13.14 | 18.71 | -176.5 | 9.01 | -206 | 46 |
| Emberiza_cirlus | 173 | 29 | -0.77565 | S | -129.5 | 8.5 | 51.2 | 50.12 | 115 | 162.5 | -9.5 | 75.5 |
| Falco_collumbarius | 597 | 691 | 0.063504 | N | 21 | 41.5 | -19.42 | -83.26 | 11.1 | -0.5 | 19.5 | 75.5 |
| Ficedula_hypoleuca | 546 | 732 | 0.127318 | S | -57 | -22.5 | 151.49 | -28.39 | 130.5 | -10 | -77.5 | 73 |
| Fulica_atra | 1690 | 1603 | -0.02295 | S | 17.5 | 6 | 62.26 | -1.04 | -85 | 2.5 | -150 | 39.5 |
| Garrulus_glandarius | 1744 | 1713 | -0.00779 | S | 41 | 4 | 226.94 | -0.36 | 98.5 | 6.5 | -180 | 16 |
| Jynx_torquilla | 48 | 6 | -0.90309 | S | 5 | 533.5 | -207.32 | 471.18 | -199 | 202.5 | -520 | 8.5 |
| Lagopus_lagopus | 1082 | 944 | -0.05926 | N | 14.5 | 44.5 | 2.84 | -32.99 | 95.5 | -25.5 | -17.5 | 118.5 |
| Lagopus_mutus | 195 | 173 | -0.05199 | N | 1 | -1.5 | 1.13 | -343.05 | 2.5 | -433.5 | 0.5 | -36 |
| Lanius_collurio | 111 | 15 | -0.86923 | S | 184.83 | 429.54 | 38.36 | 390.6 | 91.5 | 121.5 | -139.83 | 105.17 |
| Larus_canus | 848 | 612 | -0.14164 | N | -0.5 | -89.5 | -11.17 | -207.58 | -7.5 | -214 | -9 | 131 |
| Larus_ridibundus | 842 | 700 | -0.08021 | N | 4 | -9.5 | -26.99 | -34.37 | -47 | -15 | -11 | -59 |
| Loxia_curvirostra | 302 | 709 | 0.370639 | N | 90 | -10 | 178.05 | -42.68 | 75.5 | -16.5 | -6 | -10 |
| Loxia_scotica | 162 | 59 | -0.43866 | N | -54.5 | 275.5 | -62.52 | -274.64 | -75.5 | -65.5 | -29 | 211 |
| Lucustella_naevia | 1881 | 1188 | -0.19957 | S | -12 | 12 | 67.81 | 7.51 | 34 | 19.5 | -219 | 4 |
| Lullula_arborea | 196 | 73 | -0.42893 | S | -54 | 35 | 184.99 | 24.28 | 110 | 94 | -89 | 11.5 |
| Luscinia_megarhynchos | 639 | 457 | -0.14558 | S | -29 | -3.5 | 421.51 | -1.83 | 217.5 | -35.5 | 4.5 | 2.5 |
| Mergs_serrator | 665 | 674 | 0.005838 | N | -11.5 | -23 | -7.12 | -210.37 | -1 | -205 | 5 | 140 |
| Motacila_cinerea | 1845 | 1979 | 0.030449 | S | 41.5 | 9.5 | 164.61 | -1.88 | 99 | 16.5 | -11.5 | 16.5 |
| Motacilla_flava | 1155 | 1047 | -0.04264 | S | -10 | 7.5 | 304.99 | -12.24 | 73.5 | -33.5 | -43.5 | 0 |
| Numenius_arquata | 1945 | 1892 | -0.012 | N | -0.5 | -14.5 | -2.09 | -15.65 | 3.5 | 2 | 3.5 | 84.5 |
| Oenanthe_oenanthe | 1862 | 1737 | -0.03018 | N | 0 | 15 | -3.31 | -0.41 | 3 | 45.5 | 3 | 140 |
| Panurus_biarmicus | 45 | 60 | 0.124939 | S | 2 | -44.5 | 295.21 | -35.62 | 61.1 | -28.5 | 123 | -25.5 |
| Parus_cristatus | 46 | 51 | 0.044812 | N | 2.5 | 5.5 | 6.14 | -400.6 | -36 | -415.5 | -57 | -578 |
| Parus_montanus | 1220 | 1100 | -0.04497 | S | -55 | 6 | 317.33 | -0.43 | 120.5 | -28 | -115.5 | 11 |
| Parus_palustris | 1366 | 1133 | -0.08122 | S | 8 | 5.5 | 281.62 | 1.22 | 102.5 | 5.5 | -43 | -13.5 |
| Passer_montanus | 1675 | 1346 | -0.09497 | S | -86.5 | 13.5 | 36.27 | -2.82 | -76 | -30 | -128 | 4.5 |
| Phoenicurus_ochrurus | 68 | 103 | 0.180328 | S | 104.5 | -20 | 535.3 | -13.78 | 180.5 | -23 | 251 | -52 |
| Phoenicurus_phoenicurus | 1661 | 1327 | -0.0975 | S | 6 | 11 | 78.96 | 8.21 | 81.5 | -4.5 | -10.5 | 32 |
| Phylloscopus_sibilatrix | 1230 | 1270 | 0.013899 | S | 0.5 | 3 | 146.54 | -6.04 | 54 | -9 | -41.5 | -4 |
| Pica_pica | 1940 | 1958 | 0.004011 | S | 15 | 3 | 161.06 | -2.92 | 41 | 11.5 | -295 | -3 |
| Picus_viridis | 1622 | 1555 | -0.01832 | S | 69.5 | 6 | 254.26 | -2.3 | 118.5 | 13 | -125.5 | -7 |
| Pluvialis_apricaria | 849 | 784 | -0.03459 | N | 0.5 | 19.5 | -7.75 | -123.86 | -24.5 | -115 | -5 | 85.5 |
| Podiceps_cristatus | 762 | 892 | 0.06841 | S | 9 | -16 | 260.26 | -15.64 | 66.5 | -45.5 | -40.5 | -18 |
| Porzana_porzana | 39 | 26 | -0.17609 | N | -180 | 215.5 | -256.3 | 124.54 | -145.5 | 221.5 | -416.5 | -60 |
| Rallus_aquaticus | 632 | 420 | -0.17747 | S | 26.5 | 1 | 101.76 | 8.6 | 6 | 5 | -450 | 0.5 |
| Saxicola_torquata | 1215 | 1034 | -0.07006 | N | 11 | 7 | 62.76 | 4.83 | 206 | 17.5 | 49 | 0.5 |
| Scolopax_rusticola | 1693 | 1204 | -0.14803 | S | 7.5 | 10 | 65.1 | -15.14 | 74 | -7 | -54.5 | 17.5 |
| Silvia_curruca | 1094 | 1271 | 0.065128 | S | 115 | -7.5 | 362.83 | -10.66 | 130.5 | -16 | -213.5 | 13 |
| Streptopelia_turtur | 1252 | 940 | -0.12448 | S | -162.5 | 9 | 96.73 | 5.14 | 67.5 | -5.5 | -234 | 12.5 |
| Sylvia_borin | 1833 | 1867 | 0.007982 | S | 14 | 1.5 | 185.66 | -4.86 | 86 | 2.5 | -201.5 | 10 |
| Tachybaptus_ruficollis | 1366 | 1275 | -0.02994 | S | 6 | 17.5 | 104.32 | 6.95 | -61.5 | -2 | -217 | 30 |
| Tetrao_tetrix | 603 | 432 | -0.14483 | N | -15 | 88.5 | 24.3 | -63.58 | 50.5 | -30.5 | -13 | 53.5 |
| Tetrao_urogallus | 182 | 66 | -0.44053 | N | -25.5 | 40 | -13.42 | -67.4 | 19 | -217.5 | -3 | -23 |
| Tringa_nebularia | 253 | 243 | -0.01751 | N | 43 | 0.5 | 13.62 | -559.1 | 110.5 | -290.5 | 188 | -29 |
| Tringa_totanus | 1671 | 1472 | -0.05507 | N | 10 | -23 | -5.45 | -24.42 | -3 | -1.5 | -140 | -4 |
| Turdus_iliacus | 111 | 136 | 0.088216 | N | 40 | -203 | 10.81 | -551.97 | 49.5 | -323 | 155 | -341 |
| Turdus_torquatus | 745 | 544 | -0.13656 | N | -8 | 48 | 6.21 | -15.43 | 61 | 21.5 | -30.5 | 125.5 |
| Tyto_alba | 1777 | 1109 | -0.20476 | S | -0.5 | 10.5 | 112.74 | 4.41 | 10.5 | 8.5 | -174 | 3.5 |

# TableB-3 5

| Species-Name | Occ.t1 | Occ.t2 | Occupancy | Range | Obs-Leading | Obs-Rear ed | Null-Leadin | Null-Rear ec | Lnd-Leading | Lnd-Rear ed | Clim-Leadin | Clim-Rear edge |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Accipiter_nisus | 1823 | 2339 | 0.077271 | S | 41.00 | 1.50 | 222.45 | -5.58 | 37.50 | 7.50 | -21.00 | -9.50 |
| Acrocephalus_palustris | 21 | 45 | -0.14613 | S | 540.00 | 61.50 | 570.69 | 43.60 | 126.34 | 138.84 | -33.66 | -21.16 |
| Acrocephalus_scirpaceus | 775 | 1087 | 0.008325 | S | 169.00 | -17.50 | 570.68 | -7.15 | 312.00 | -5.00 | -11.50 | 11.50 |
| Actitis_hypoleucus | 1406 | 1211 | 0.005525 | N | -7.50 | 5.00 | 8.99 | -44.18 | 104.50 | -68.00 | -118.00 | 87.00 |
| Alcedo_athis | 1305 | 1331 | -0.02783 | S | 94.00 | -2.50 | 331.75 | -7.88 | 167.00 | -11.50 | -153.50 | 2.00 |
| Alectoris_rufa | 919 | 1636 | 0.120903 | S | 169.50 | -48.50 | 398.46 | -50.12 | 75.00 | -46.00 | -228.50 | -7.00 |
| Anas_acuta | 86 | 65 | -0.00508 | N | 1.00 | 24.50 | -82.26 | 4.27 | -36.50 | -23.50 | 41.50 | -19.00 |
| Anas_clypeata | 520 | 511 | -0.05895 | S | 81.50 | -2.50 | 71.57 | -23.17 | -106.50 | -43.50 | -39.00 | 8.00 |
| Anas_crecca | 1376 | 1184 | -0.07943 | N | 84.50 | -1.50 | 32.48 | -18.18 | -78.00 | 20.00 | -56.50 | 142.50 |
| Anas_penelope | 283 | 352 | 0.104516 | N | 88.00 | -33.50 | 23.91 | -96.88 | 53.00 | -52.50 | 22.00 | -1.00 |
| Anas_querquedula | 136 | 197 | 0.00634 | S | 239.00 | 1.50 | 415.69 | -8.75 | 85.50 | 10.50 | -83.00 | 18.00 |
| Anas_strepera | 158 | 713 | 0.354011 | S | 191.00 | -62.50 | 322.53 | -70.06 | 56.50 | -57.50 | -32.00 | -5.50 |
| Anser_anser | 200 | 1665 | 0.555094 | N | 235.50 | -90.50 | 223.94 | -148.23 | 170.00 | -71.50 | 12.00 | -21.00 |
| Anthus_trivialis | 1793 | 1268 | -0.0706 | S | -6.00 | 9.00 | 66.26 | -2.31 | 20.00 | -3.50 | -28.50 | 16.50 |
| Ardea_cinerea | 1686 | 1931 | 0.141429 | N | -13.50 | -9.50 | 187.44 | -15.03 | 13.00 | -3.00 | -38.00 | 38.50 |
| Asio_flammeus | 800 | 413 | -0.07122 | N | -15.50 | -5.00 | -14.79 | -61.45 | 87.50 | -88.00 | 1.50 | 111.00 |
| Asio_otus | 590 | 491 | -0.12249 | N | -33.50 | 1.00 | 44.64 | -25.97 | -63.00 | -22.00 | -87.00 | 52.50 |
| Athene_noctua | 1381 | 1236 | -0.051 | S | -18.50 | 29.50 | 330.84 | 1.20 | 210.00 | 10.00 | -90.00 | 5.50 |
| Aythya_ferina | 512 | 317 | -0.00085 | S | -58.50 | 0.00 | 91.14 | -4.90 | -1.50 | -35.50 | -50.00 | 10.50 |
| Aythya_fuligula | 1290 | 1715 | 0.060844 | S | 87.00 | -28.50 | 93.66 | -38.88 | -157.00 | -32.50 | -160.00 | 3.00 |
| Caprimulgus_europeaeus | 562 | 326 | -0.31199 | S | -136.50 | 2.50 | 157.94 | 9.89 | 11.00 | 15.00 | -328.50 | 11.50 |
| Carduelis_cabaret | 1979 | 1543 | -0.05242 | N | 32.50 | -9.00 | 89.85 | -23.56 | 14.50 | -32.00 | -9.00 | 90.00 |
| Carduelis_flavirostris | 656 | 534 | -0.00332 | N | 1.50 | 10.50 | -11.06 | -260.90 | -6.00 | -257.00 | -9.50 | 0.00 |
| Carduelis_spinus | 625 | 1778 | 0.267829 | N | 65.00 | -70.00 | 223.14 | -87.23 | 18.00 | -52.50 | 12.50 | 261.00 |
| Charadrius_dubius | 288 | 595 | 0.163857 | S | 221.50 | -49.50 | 508.12 | -80.82 | 118.00 | -63.00 | 1.00 | 9.50 |
| Cinclus_cinclus | 1434 | 1297 | -0.03961 | N | -9.00 | -2.00 | 50.34 | -2.60 | 123.50 | 3.50 | -2.00 | 4.50 |
| Coccothraustes_coccothraustes | 459 | 113 | -0.1635 | S | -122.50 | 13.50 | 104.03 | 21.95 | 97.50 | -31.00 | -118.50 | -8.00 |
| Columba_livia | 1498 | 2218 | 0.143594 | N | 0.00 | -4.50 | 1.25 | -8.09 | 7.00 | 16.00 | 3.00 | 4.00 |
| Columba_orenas | 1956 | 1918 | -0.03106 | S | 9.50 | 3.00 | 174.25 | -1.33 | 114.50 | 7.00 | -195.00 | 12.50 |
| Corvus_corax | 1243 | 1985 | -0.04139 | N | 2.00 | -1.50 | 2.32 | -4.15 | 9.00 | 25.00 | 1.00 | -5.50 |
| Coturnix_coturnix | 405 | 858 | 0.297801 | S | 247.50 | 24.00 | 231.27 | 6.77 | 26.00 | -3.00 | -103.00 | -15.00 |
| Crex_crex | 659 | 184 | -0.61206 | N | -29.50 | 374.50 | -100.33 | 48.59 | -46.00 | 110.50 | -118.00 | 220.50 |
| Dendrocopus_minor | 889 | 559 | -0.05127 | S | -33.00 | 32.00 | 424.52 | 13.67 | 340.00 | -1.50 | -44.50 | 0.50 |
| Emberiza_calandra | 1357 | 592 | -0.16832 | S | -203.00 | 49.00 | -69.77 | 23.36 | -164.00 | 9.00 | -182.50 | 16.00 |
| Emberiza_cirlus | 173 | 26 | -0.77565 | S | -161.50 | 9.00 | -0.21 | 55.11 | 174.50 | 180.00 | -66.00 | 66.50 |
| Falco_collumbarius | 597 | 663 | 0.063504 | N | 21.00 | 44.00 | -22.37 | -78.92 | -14.00 | -48.50 | 13.00 | 84.50 |
| Ficedula_hypoleuca | 546 | 534 | 0.127318 | S | -59.00 | -15.00 | 105.39 | -16.64 | 167.00 | -20.50 | -38.50 | 28.00 |
| Fulica_atra | 1690 | 1625 | -0.02295 | S | 6.00 | -4.50 | 69.40 | -2.87 | -95.50 | -0.50 | -153.00 | 41.50 |
| Garrulus_glandarius | 1744 | 1987 | -0.00779 | S | 77.00 | 1.00 | 338.73 | -3.71 | 139.50 | 7.00 | -192.00 | 5.50 |
| Jynx_torquilla | 48 | 13 | -0.90309 | S | 46.15 | 574.65 | -218.69 | 379.81 | -105.00 | 313.50 | -290.00 | 238.50 |
| Lagopus_lagopus | 1082 | 847 | -0.05926 | N | 63.00 | 66.50 | -5.67 | -21.59 | 75.00 | -35.50 | -73.50 | 115.50 |
| Lagopus_mutus | 195 | 175 | -0.05199 | N | -2.00 | 5.50 | 0.87 | -233.37 | -10.50 | -416.00 | -3.00 | -11.50 |
| Lanius_collurio | 111 | 22 | -0.86923 | S | 173.00 | 336.00 | 126.40 | 295.88 | -38.50 | 206.50 | -167.16 | 77.84 |
| Larus_canus | 848 | 757 | -0.14164 | N | 0.00 | 4.00 | -7.21 | -241.22 | -13.50 | -230.50 | 1.50 | 207.00 |
| Larus_ridibundus | 842 | 997 | -0.08021 | N | 0.50 | -18.00 | -8.30 | -58.18 | -12.50 | -21.50 | 7.00 | 146.00 |
| Loxia_curvirostra | 302 | 1017 | 0.370639 | N | 39.50 | -17.50 | 215.62 | -55.38 | 25.50 | -26.50 | 19.00 | -3.00 |
| Loxia_scotica | 162 | 49 | -0.43866 | N | -74.00 | 273.50 | -77.06 | -190.59 | -114.00 | -208.50 | -62.00 | 183.50 |
| Lucustella_naevia | 1881 | 1660 | -0.19957 | S | 38.00 | 6.50 | 157.62 | 2.03 | -20.50 | 16.50 | -415.00 | 8.00 |
| Lullula_arborea | 196 | 155 | -0.42893 | S | 92.50 | 36.00 | 568.54 | 18.52 | 329.00 | 67.50 | -79.00 | 15.00 |
| Luscinia_megarhynchos | 639 | 363 | -0.14558 | S | -16.50 | 9.00 | 405.27 | 3.55 | 350.00 | -19.50 | -4.50 | 0.00 |
| Mergs_serrator | 665 | 535 | 0.005838 | N | -8.50 | -10.00 | -22.06 | -192.21 | -4.00 | -181.50 | 8.00 | 27.50 |
| Motacila_cinerea | 1845 | 2188 | 0.030449 | S | 71.00 | 1.00 | 209.84 | -2.47 | 23.50 | 13.00 | 4.00 | 3.50 |
| Motacilla_flava | 1155 | 782 | -0.04264 | S | -26.00 | 35.00 | 271.06 | -5.16 | 210.00 | -31.00 | -45.50 | 1.50 |
| Numenius_arquata | 1945 | 1620 | -0.012 | N | 0.50 | 26.00 | -5.39 | -6.56 | 3.50 | -9.50 | 0.00 | 83.50 |
| Oenanthe_oenanthe | 1862 | 1606 | -0.03018 | N | 0.00 | 7.00 | -5.25 | 2.34 | 3.00 | 42.00 | 3.00 | 130.50 |
| Panurus_biarmicus | 45 | 80 | 0.124939 | S | 130.50 | -48.50 | 440.69 | -32.90 | 205.50 | 21.50 | 37.50 | -26.50 |
| Parus_cristatus | 46 | 59 | 0.044812 | N | 2.50 | -2.50 | 12.25 | -402.15 | -51.00 | -549.00 | -11.50 | -33.50 |
| Parus_montanus | 1220 | 557 | -0.04497 | S | -80.00 | 24.00 | 211.10 | 8.05 | 176.00 | -24.00 | -95.50 | 12.50 |
| Parus_palustris | 1366 | 1067 | -0.08122 | S | -12.50 | 9.50 | 255.36 | 3.10 | 213.50 | 7.50 | -64.50 | -2.50 |
| Passer_montanus | 1675 | 999 | -0.09497 | S | -98.00 | 52.50 | 8.17 | 30.37 | -82.50 | -32.50 | -192.00 | 10.00 |
| Phoenicurus_ochrurus | 68 | 128 | 0.180328 | S | 252.50 | -31.50 | 576.25 | -22.44 | 312.50 | -15.00 | -27.00 | 4.50 |
| Phoenicurus_phoenicurus | 1661 | 1142 | -0.0975 | S | -15.00 | 3.50 | 47.31 | -0.37 | 19.00 | -19.50 | -10.00 | 27.50 |
| Phylloscopus_sibilatrix | 1230 | 800 | 0.013899 | S | -31.50 | 9.50 | 65.70 | 1.30 | 21.50 | -16.50 | -43.00 | -12.50 |
| Pica_pica | 1940 | 2079 | 0.004011 | S | 26.00 | 0.00 | 223.65 | -1.23 | 106.00 | 11.50 | -251.00 | 0.00 |
| Picus_viridis | 1622 | 1638 | -0.01832 | S | 42.50 | 7.00 | 286.36 | -0.13 | 161.50 | 9.50 | -189.00 | -7.00 |
| Pluvialis_apricaria | 849 | 681 | -0.03459 | N | 1.50 | 28.50 | -11.22 | -106.55 | -26.00 | -123.50 | -9.00 | 54.00 |
| Podiceps_cristatus | 762 | 1001 | 0.06841 | S | -8.00 | -37.00 | 292.51 | -43.98 | 105.50 | -50.50 | -54.50 | -10.50 |
| Porzana_porzana | 39 | 40 | -0.17609 | N | -22.50 | 28.00 | -107.07 | -0.86 | -184.50 | 166.50 | 117.50 | 439.00 |
| Rallus_aquaticus | 632 | 676 | -0.17747 | S | 147.50 | -4.50 | 163.08 | -5.57 | -24.00 | 15.00 | -403.50 | 31.00 |
| Saxicola_torquata | 1215 | 878 | -0.07006 | N | -31.50 | 67.50 | 74.97 | 9.29 | 183.00 | 17.50 | -25.50 | 3.50 |
| Scolopax_rusticola | 1693 | 850 | -0.14803 | S | -4.50 | 19.00 | 31.46 | 3.21 | 25.50 | -27.00 | -35.50 | 22.00 |
| Silvia_curruca | 1094 | 1451 | 0.065128 | S | 175.00 | -18.50 | 399.18 | -18.41 | 165.50 | -19.00 | -113.50 | 2.50 |
| Streptopelia_turtur | 1252 | 613 | -0.12448 | S | -262.00 | 30.00 | -34.45 | 15.70 | 105.00 | -7.50 | -198.50 | 9.50 |
| Sylvia_borin | 1833 | 2057 | 0.007982 | S | 0.00 | -1.00 | 227.58 | -6.20 | 15.50 | 2.50 | -229.50 | 9.00 |
| Tachybaptus_ruficollis | 1366 | 1683 | -0.02994 | S | 35.00 | -8.50 | 172.90 | -12.15 | -56.50 | -1.00 | -195.00 | 33.00 |
| Tetrao_tetrix | 603 | 432 | -0.14483 | N | -14.50 | 151.50 | 27.40 | -73.84 | 5.00 | -86.50 | 4.00 | 69.50 |
| Tetrao_urogallus | 182 | 51 | -0.44053 | N | -14.00 | 84.00 | -21.50 | -60.20 | -44.50 | -236.50 | 5.00 | 26.50 |
| Tringa_nebularia | 253 | 257 | -0.01751 | N | 33.00 | 20.00 | 14.26 | -564.45 | 72.50 | -387.50 | 199.00 | -60.00 |
| Tringa_totanus | 1671 | 961 | -0.05507 | N | 8.00 | 8.50 | -42.26 | -8.07 | -9.50 | -11.00 | -140.00 | 12.50 |
| Turdus_iliacus | 111 | 74 | 0.088216 | N | 80.00 | 78.50 | -18.58 | -434.06 | -3.50 | -335.00 | 157.50 | 7.50 |
| Turdus_torquatus | 745 | 424 | -0.13656 | N | -38.00 | 44.50 | -2.57 | 8.06 | -6.00 | 3.00 | -21.00 | 105.00 |
| Tyto_alba | 1777 | 1892 | -0.20476 | S | 93.50 | -1.50 | 264.96 | -3.33 | 27.00 | 8.50 | -274.50 | 16.50 |

# APPENDIX D. CHAPTER IV

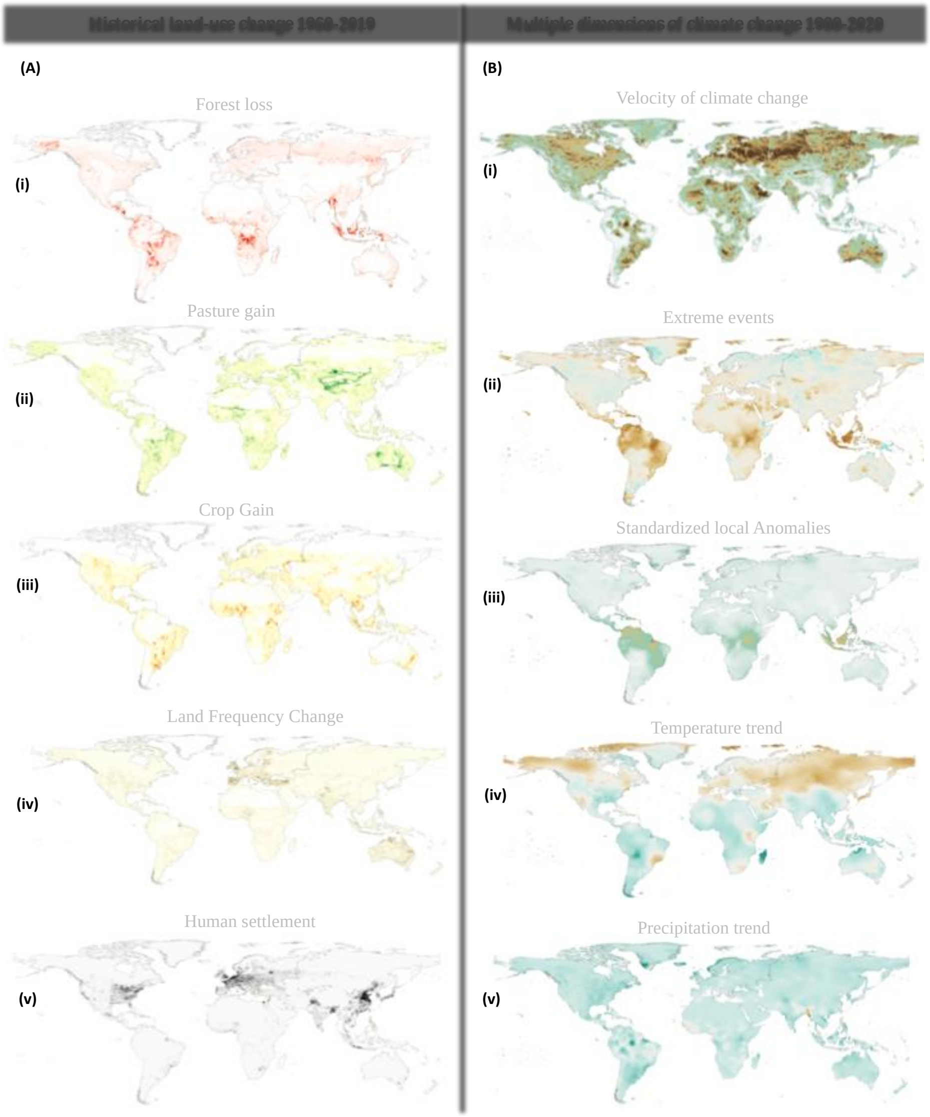


**Fig D-5 1.** Multiple dimensions of climate and land-use change over the last century. Panel (A) shows the historical land change for (i) forest loss; (ii) pasture gain; (iii) crop-gain; (iv) land frequency change; (v) human settlements. Dark colours on the map correspond to the high level of change. Panel (B) shows five metrics of climate change, (i) velocity; (ii) extreme events; (iii) standardized local anomalies; (iv) temperature trend and (v) precipitation trend. Dark brown colours correspond to the high level of climate change. For precipitation trend, dark brown corresponds to decreased precipitation and dark blue indicates increased precipitation over the past century.